

**POPULATION DYNAMICS, HABITAT USE AND
MOVEMENTS OF GREATER SAGE-GROUSE IN MOFFAT
COUNTY, COLORADO**

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ABSTRACT

Long-term declines in greater sage-grouse (*Centrocercus urophasianus*) abundance may be associated with low productivity due to habitat degradation. Therefore, I investigated the effects of vegetation characteristics on nest site selection and success, and created predictive models using forward stepwise logistic regression. Greater sage-grouse nested in sites having greater sagebrush canopy cover, nest shrub height and visual obstruction than random sites. Forb cover was greater at nest sites than random but grass cover and % exotic species at the nest bowl were greater at random sites than nest sites.

Nest success was high with 58% ($n = 108$) of hens hatching ≥ 1 egg. Nest success was positively associated with plant species richness, percent sagebrush, grass and forb cover and negatively associated with exotic herbaceous cover. Additionally, grass heights measured at the nest bowl and at 1 m from the nest bowl were parameters associated with nest success. Vegetation was reduced in 2002, a year with less spring precipitation, and may be associated with lower nest success. Habitat management to encourage greater sage-grouse nest success should promote native herbaceous understory growth in April and May and discourage sagebrush removal.

Habitat management guidelines are based, in part, on studies of greater sage-grouse nest site selection, which measure habitat characteristics post-hatch, > 30 days after initiation. Thus, these recommendations may be flawed due to the time lag in sampling. I investigated differences in habitat at initiation versus hatch using previous year's nest sites. A randomized complete block MANOVA indicated differences based on timing of sampling. The difference was largely due to grass height and percent grass cover. Grass heights at the nest bowl and at 1 m were 10 cm and 9 cm at initiation and 16 cm and 13 cm at hatch,

respectively. Percent grass cover of the sample plot increased from 4 to 6% cover from initiation to hatch. Sampling techniques conducted at hatch sufficiently describes nest site habitat at selection apart from grass heights and grass cover.

Despite extensive research into the habitat requirements of greater sage-grouse, summer night-roosting habitat has received no attention. Therefore, I investigated the vegetation characteristics of brood and night roost selection and compared diurnal and nocturnal habitat use and selection. Predictive models were created using forward stepwise logistic regression. Greater sage-grouse selected brood-use areas with greater visual obstruction, greater forb cover and less bare ground than random.

Night-roost locations were characterized by less bare ground and visual obstruction but greater percent forb cover than at random sites. Mean shrub cover and shrub height at night roost locations was lower (9% vs. 22%) and shorter (31 vs. 58 cm) than at brood sites. Forb cover was an important predictor of both diurnal and nocturnal habitat use but did not meet the minimum requirements of $\geq 10\%$ suggested by management guidelines. Current habitat management guidelines attend only to diurnal habitat needs and should be revised in order to address the variance in temporal habitat selection.

I described home range, daily movements and survival of greater sage-grouse monthly, seasonally and annually. Median daily movement during the brood-rearing period was greater for females with broods (184 m/day) than those without broods (103 m/day), and was not associated with chicks/female at 6 weeks post-hatch. Lek to nest distance and brood home range sizes were greater for females that nested in the Axial Basin (4.6 km, 1,151 ha) than the Danforth Hills (2.6 km, 439 ha) indicating that habitat conditions may be causing greater movement in the Axial Basin. Distances moved from the last diurnal location to

night roost sites (397 m) suggested that females with broods were required to move 2 times their median daily movement in order to find suitable night-roost habitat and that seasonal movement estimates in the literature may be biased low. Annual home range sizes of yearlings and adults, and seasonal movements from the lek of capture indicated that the population of greater sage-grouse in the Axial Basin and Danforth Hills was non-migratory. Annual survival rates were greater for yearling (75%) than adult females (57%). Year, seasonal trend and age were variables that contributed to predictive annual survival models. Survival rates were lowest in the breeding and brood-rearing periods and increased through the fall and winter.

Body condition indices, serum chemical constituents and disease prevalence were estimated for pre-laying female greater sage-grouse. Previous studies conjectured pre-maternal diet was associated with greater sage-grouse productivity and survival but gave no specifics on condition with respect to body size or serum biochemical constituents. Thus I investigated pre-breeding body condition as a function of a body condition index and a serum chemical panel and how these parameters were associated with reproduction and survival. No differences were found in measures of fecundity, however the expense may be incurred through survival rates, which were related to the body condition index, serum protein and uric acid concentrations. Baseline biochemistry reference ranges for pre-breeding hens were established. These values varied by year and capture technique. Annual variation may be linked to precipitation and forage quality. Elevated creatinine kinase and chloride levels occurred in females captured by the CODA net-launcher in comparison to females captured by night-spotlighting. Differential biochemical values may have been caused by stress or diurnal variation in serum chemistry.

Diseases tested included avian influenza, *Salmonella pullorum*/ *S. typhoid*, *Mycoplasma gallisepticum*, *M. synoviae*, and *M. meleagridis*. Individual grouse tested positive for *M. synoviae*, however there was no consistency of lab results among years, laboratories, or blood storage method. Additionally, no relationship between disease occurrence and reproduction or survival was detected and false positives have been reported with the plate agglutination-screening test. Given this information, the serology results need to be viewed cautiously as they were based on questionable disease incidence.

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INTRODUCTION

Greater sage-grouse are the largest grouse in North America. The Latin name, *Centrocercus urophasianus*, is derived from the greek word "kentron" meaning spiny, "kerkos" meaning tail, and "oura phasianos" meaning tail of a pheasant (Gill 1966). *Centrocercus* is one of 10 genera in the sub-family Tetraonidae, of the order Galliformes (fowl-like birds). They are members of the family Phasianidae to which the turkey (*Meleagris* spp.), quail (*Callipepla* spp.), partridge (*Alectoris* spp.), pheasant (*Phasianus* spp.) and grouse belong (Madge and McGowan 2002).

There are 2 species of sage-grouse in the genera *Centrocercus* (Young et al. 2000), the greater sage-grouse and Gunnison sage-grouse, *Centrocercus minimus*. Two weakly described subspecies include Eastern (*C. u. urophasianus*) and Western (*C. u. phaois*) greater sage-grouse (Hupp and Braun 1991, Schroeder et al. 1999).

Sage-grouse depend on sagebrush (*Artemisia* spp.) for food or cover at all times of the year. Their distribution is associated with habitat dominated by sagebrush in western North America (Schroeder et al. 1999). Greater sage-grouse have been reduced to populations in southeastern Oregon, northeast and east border of California, southern Idaho, northern two-thirds of Nevada, portions of northeast, north and south Utah, portions of western Colorado, Wyoming (except northwest and southeast corners), east and southwest Montana, northwest and southwest S. Dakota, North Dakota, southeastern Alberta, southwestern Saskatchewan, and small populations in central Washington (Schroeder et al. 1999). Gunnison sage-grouse are found in 8 isolated populations in Southwestern Colorado and adjacent San Juan County, Utah (Young et al. 2000).

Greater sage-grouse have experienced continued declines from the early 1900's to present with relief in the 1940's and 1950's (Hornady 1916, Patterson 1952, Autenrieth 1981, Connelly et al. 2000). It is estimated that breeding populations have declined by 17-47% in the last 30 years (Connelly and Braun 1997). All populations of greater sage-grouse are under review for listing under the Endangered Species Act (Connelly et al. 2000). In Canada, greater sage-grouse have been listed provincially as endangered or threatened (Aldridge 2000).

Within Colorado, greater sage-grouse historically occurred in at least 23 and possibly 27 counties (Braun 1995). Northern Colorado held and holds the highest density of greater sage-grouse and sagebrush habitat (Braun 1995). Currently, there are 15 counties in which greater sage-grouse occur in Colorado and populations are considered as persistent (> 500 breeding birds) in only 5 of these (Braun 1995). Braun (1998) noted lek count declines of 45 and 82% in Colorado since 1980.

Lek surveys indicating population trends have been conducted in Moffat County from 1958-1997 and on Colowyo mine property in the Axial Basin in 1981, 1983 and 1994 to present (Hoffman 1979, Braun 1998, Monarch 2000). Mean number of males per lek has declined in Moffat County since the late 1960's. Braun (1998) reported an 82% decrease in the number of males on strutting grounds from 1978-1998 and a 52% decline in the number of active leks.

Other than declining population trends, little is known of the Axial Basin and Danforth Hills population of greater sage-grouse. The objectives of my research were to (1) estimate reproductive parameters and nesting and brood-rearing habitat use; (2) characterize night-roost habitat selection; (3) assess current nest habitat sampling techniques; (4) ascertain

annual and seasonal movements, home-range sizes, cause-specific mortality and survival; and (5) assess pre-breeding hen body condition and disease prevalence and their possible influences on productivity and survival.

STUDY AREA

The central part of my study area was the Axial Basin and Danforth Hills, located in Moffat County, 30 km southwest of Craig, Colorado. The topography consisted of rolling hills and the study area was approximately 200,000 ha in area. The Axial Basin and Danforth Hills comprised approximately 36,000 ha and 52,000 ha of the study area, respectively. Elevation in the Axial Basin and Danforth Hills ranged from 1,818 – 2,000 m and 2,001 – 2,388 m, respectively. The Yampa River flows from east to west through the Axial Basin. The climate of Moffat County is semi-arid, receiving 20.3 to 50.8 cm of annual precipitation. The mean annual temperature was 6.3 C (Braun and Hoffman 1979). The landscape consisted of private, state, and federally owned/administered sagebrush rangeland (*Artemisia tridentata*), pinyon (*Pinus edulis*)-juniper (*Juniperus monosperma*, *J. osteosperma*, *J. scopulorum*), mountain shrub communities with Gambel's oak (*Quercus gambelii*), serviceberry (*Amelanchier* sp.), snowberry (*Symphoricarpos oreophilus*) chokecherry (*Prunus virginiana*), and aspen (*Populus tremuloides*), private agricultural land in the Conservation Reserve Program (CRP), active strip mines, reclaimed strip mine lands, and agricultural lands. The sagebrush community was dominated by an overstory of big sagebrush (*A. tridentata*) and snowberry. The predominant grasses within this community included western wheatgrass (*Pascopyron smithii*), Kentucky bluegrass (*Poa pratensis*), Sandberg bluegrass (*Poa secunda*), cheatgrass brome (*Bromus tectorum*), and needle and

thread grass (*Hespero-stipa comata*). Dominant forbs included lupine (*Lupinus sericeus*), wild onion (*Allium* spp.), arrowleaf balsamroot (*Balsamorhiza sagittata*), and yarrow (*Achillea millefolium*).

GENERAL METHODS

Lek Surveys

Active leks were surveyed a minimum of 3 times from 17 March to 8 May. Colorado Division of Wildlife protocol (2001) was used to survey 16 leks in the Axial Basin and Danforth Hills.

Capture

Grouse were captured on or near 11 lek sites during April and May 2001/2002. Three methods of trapping were employed, night-time spotlighting by vehicle and backpack, walk-in traps, and a CODA net-launcher. Individuals were sexed and aged as yearlings or adults using wing characteristics (Dalke et al. 1963). They were banded and radio-tagged with necklace-mounted transmitters (Leonard et al. 2000) equipped with 4-hour mortality sensors and a range of 1.5 km. Guaranteed battery life was 18 months and a 30-cm antenna lay between the wings and down the back of the bird. A hand-held Yagi antenna, attached to a receiver/scanner was used to locate the radio-tagged grouse. Morphological characteristics of grouse measured at time of capture included weight and keel length. Blood was taken from the cutaneous ulnar vein for disease and biochemical analysis.

Monitoring

Females were monitored until nesting was evident. Nest fate was determined when monitoring indicated that nesting efforts had ceased. Nests were categorized as successful (≥ 1 egg hatched) or unsuccessful (Wallestad and Pyrah 1974). During the spring and summer, females with broods were located 1-2 times a week. Locations were collected for each brood from the time of hatch to 10 weeks because at this age chicks are considered independent from the hen (N. Burkepile, personal communication). Hens without broods were located weekly. During the fall and winter, locations were obtained on all birds ≥ 1 time per month. Grouse status (alive/dead) was monitored weekly. All use locations were recorded in Universal Transverse Mercator (UTM) coordinates using a hand-held Global Positioning System (GPS). Female body mass was analyzed using a 2-way factorial ANOVA (Ott and Longnecker 2001) to determine whether body mass varied with age or year.

GENERAL RESULTS

Lek Surveys

We attempted to record peak attendance days in 2001 and 2002 (Table 0.1). Peak female attendance occurred in the first week of April and was similar among years. Two potential leks, Tic Tac and East Box Elder, found in 2001 were inactive in 2002. Additionally, historical Temple Gulch lek was found inactive when surveyed in 2002. Historical lek sites SG- 1- 3, 5 and 6, were devoid of males both years. Dramatic declines in male attendance from 2001 to 2002 were observed at West Box Elder Lek. Domestic sheep occupied this lek from 28 March to 10 May in 2002.

Capture

In March and April 2001 and 2002 I captured 144 grouse. One hundred sixteen grouse (81%) were captured using the spot-light capture method, 26 (18%) were captured using the CODA net launcher and 2 were captured using walk-in-traps (Table 0.2). One hundred females and 15 males were radio-marked and 6 were re-captures. The remaining grouse were captured in order to validate our blood testing procedures. Of the radio-marked females, 54 were adults and 46 were yearlings.

Body mass

Mean body mass of yearling females was 1,424 g ($SE = 19$, $n = 27$) in 2001, and 1,426 g ($SE = 15$, $n = 19$) in 2002. Body mass of adult greater sage-grouse females was 1,625 g ($SE = 20$, $n = 35$) and 1,564 g ($SE = 24$, $n = 22$) for 2001 and 2002, respectively. Weights did not vary between years ($F = 3.12$, $P = 0.0805$). However, yearling female weight (1,425 g, $SE = 13$, $n = 46$) was less ($F = 72.01$, $P < 0.001$) than that of adult females (1,601 g, $SE = 16$, $n = 57$).

THESIS CHAPTERS

Chapters in my thesis are written separately, with the intent of individual publication of each. Chapter 1 describes reproductive parameters and models nest site selection and success of greater sage-grouse in northwest Colorado. Additionally, this chapter includes a description of cause-specific nest depredation. Chapter 2 is a techniques chapter that evaluates the timing of nest vegetation sampling. Chapter 3 describes brood productivity and diurnal and nocturnal habitat selection of brood females. Chapter 4 reports annual and seasonal movements, cause-specific mortality and survival of greater sage-grouse females.

Chapter 5 describes the fitness of greater sage-grouse females associated with disease and the pre-breeding body condition of females.

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Table 0.1. Peak female and male lek attendance (numbers and date) for greater sage-grouse in the Axial Basin and Danforth Hills, Colorado, 2001/2002.

Lek Names	2001		2002	
	Males	Females	Males	Females
East Box Elder ^a	8 (4/1)	0	0	0
Gossard/ SG- 12	8 (4/5)	6 (4/5)	8 (3/26)	15 (3/26)
Juniper 1 ^c	0	1 (4/1)	0	4 (3/21)
Juniper 2/ SG-13	16 (3/20)	9 (4/4)	18 (4/11)	9 (4/7)
Morgan Gulch 2/ SG-10	30 (4/12)	23 (4/5)	23 (4/5)	58 (4/5)
New Juniper Gulch ^a	5 (3/28)	3 (4/3)	0	0
SG 5 ^c	0	0	0	0
SG 6 ^c	0	0	0	0
SG-1/2 ^c	0	0	0	0
SG-3 ^c	0	3 (4/6)	0	1 (4/22)
SG-4	0	0	9 (4/11)	9 (4/11)
SG-7	27 (4/8)	21 (4/3)	37 (5/4)	16 (4/9)
SG-8 ^b	4 (4/15)	3 (4/15)	1 (4/2)	0
Temple Gulch (SG-14)	7 (3/30)	0	0	0
Tic Tac ^a	4 (4/14)	0	0	0
West Box Elder/ SG-11	33 (3/25)	52 (4/1)	15 (3/25)	38 (4/3)

^a Potential lek 2001

^b UTM coordinates different from Monarch (2000)

^c Historical lek site

Table 0.2. Greater sage-grouse captures by year, sex and capture technique in northwestern Colorado, 2001 and 2002.

	2001			2002	
	Spotlighting	CODA net launcher	Walk-in-trap ^a	Spotlighting	CODA net launcher
Females	52	12	2	31	11
Males	12	3	0	21	0
TOTALS	64	15	2	52	11

^a Capture technique attempted only in 2001

CHAPTER 1. NEST SITE SELECTION AND SUCCESS OF GREATER SAGE- GROUSE IN NORTHWEST COLORADO

INTRODUCTION

There are several factors responsible for the decline in greater sage-grouse populations. The most important are habitat loss, fragmentation and degradation (Schneegas 1967, Klebenow 1972, Braun 1998, Leonard et al. 2000). Degradation of sagebrush has been ongoing since early settlement across western rangelands. Recent landscape fragmentation has favored generalist predators, thus predation pressure may have increased as a function of habitat changes (Storch and Willebrand 1991). For many grouse species, nest depredation is an important source of reduced productivity (Reynolds et al. 1988). Long-term declines in greater sage-grouse abundance may be associated with low productivity due to habitat degradation. Thus, I investigated the effects of vegetation characteristics on nest success and created models of habitat characteristics to predict nest selection and success.

Reproduction

Incubation of greater sage-grouse lasts 25 to 29 days (Schroeder 1997). Mean clutch size varies from 6.0 to 9.5 throughout the range of the species (Connelly et al. 2000) and adults tend to lay larger clutches and are more successful than yearlings (77% vs. 44%) (Wallestad and Pyrah 1974). In Oregon, peak hatching occurs from the last week of May to the second week in June (Call and Maser 1985). Braun (1981) reported peak hatching dates in southern Moffat County, Colorado to occur from 15-21 June.

Nest success reported in the literature ranged from 15% (Gregg et al. 1994) to 77% (Wallestad and Pyrah 1974) and varied with local vegetation and weather conditions (Gill 1966). Braun (1981) and Swenson (1986) stated that older females have greater nest success and less variance than yearling females. Bergerud (1988) reported an average nest success of 38% and indicated that juvenile females renested less frequently than adult females. Contrastingly, Connelly et al. (1993) found nest success (53%) and renesting rates between age classes to be similar.

Nesting habitat

Spatial variation and diversity of habitat available to a prey population are likely to enhance the stability of that population (Reynolds et al. 1988). Specifically, increased spatial understory heterogeneity and cover at nest sites reduces the risk of nest detection by predators, and protects the eggs from environmental conditions (Bowman and Harris 1980, Cambell et al. 2002). The basic requirement of a greater sage-grouse nest site is concealment (Patterson 1952). Nests are almost exclusively under sagebrush (Patterson 1952, Klebenow 1969, Braun et al. 1977, Wakkinen 1990, Connelly et al. 1991, Musil et al. 1994) and are created by scratching out a depression (Schroeder et al. 1999). Nests are infrequently constructed under other shrubs, and meet with lower success (Connelly et al. 1991).

Nests are generally under shrubs with more ground, lateral, and shrub cover than at random sites (Klebenow 1969). Successful nests tend to be in areas of higher canopy cover ($\geq 15\%$) than unsuccessful nests (Klebenow 1969, Wallestad and Pyrah 1974, Gregg et al. 1994). In North Park, Colorado, nest shrub cover averaged 44% ($n = 19$) (Schoenberg 1982). Bowman and Harris (1980) indicated canopy cover strongly influenced prey vulnerability. Medium height shrubs (30-70 cm) have been deemed important for nest success (Wallestad

and Pyrah 1974, Schoenberg 1982, Gregg et al. 1994, Delong et al. 1995, Connelly et al. 2000). Klebenow (1969), Wakkinen (1990), Gregg et al. (1994) and Delong et al. (1995) indicated tall grass cover (≥ 18 cm) as a parameter important to nest success.

METHODS

Monitoring

Radio-marked females were monitored until nesting was evident. Nest fate was determined when monitoring indicated that nesting efforts had ceased. Nests were categorized as successful (≥ 1 egg hatched) or unsuccessful (Wallestad and Pyrah 1974). Nest predators were classified as either avian or mammalian based on patterns of egg and nest site destruction (Sargeant et al. 1998). If eggs were not present or evidence was confounding, the nest predator type was classified as unknown (Larivière 1999). Nest sites were recorded in Universal Transverse Mercator (UTM) coordinates using a hand-held Global Positioning System (GPS).

Vegetation Sampling

Microhabitat refers to fine-scale habitat resolution within a patch of habitat at a nest site. These measurements were made ≤ 7 days after nesting efforts had ceased for each successful and unsuccessful nest and at an equal number of random sites. Random locations were selected from northing and easting UTM coordinates falling within the home range of the population and were measured within 1 week of vegetation sampling at the nest site use area using identical techniques. Random sites were selected from within a sagebrush community within the study site so that I could estimate the macro and micro-habitat variables selected for nesting. Ten meter transects were placed in the cardinal directions

intersecting at the center of the nest bowl. The nest shrub species and height were recorded. Canopy cover of the shrub overstory was estimated using line-intercept (Canfield 1941). Height of the nearest shrub within 1 m of the transect line was measured at 2.5 m, 5 m, 7.5 m and 10 m. Grass height (GHEIGHT) was measured for the nearest, tallest grass part at the points where the edge of the nest bowl and the transect intercept, and at the 1 m point on each transect.

Percent forbs and grass cover by lowest possible taxa, percent exotics, bare ground and litter canopy cover were estimated using 40 by 50 cm microplots (adapted from Daubenmire 1959, Mosley et al. 1989). Eleven cover classes were used as suggested by Boisvert (2002). Cover classes were delineated as: (Trace 1: 0-2%, Trace 2: 3-9%, 1: 10-19%, 2: 20-29%, 3:30-39%, 4: 40-49%, 5: 50-59%, 6: 60-69%, 7:70-79%, 8: 80-89%, 9: 90-100%). Two microplots were placed at the interception point of the transects, with 1 corner on the edge of the nest bowl going north or south along the transect. Subsequent plots were placed with the outermost corner along the transects at 2.5, 5 and 10 m.

Overhead concealment of the nest was measured using a 12 x 12 cm cover-board separated into 25, 3 x 3 cm squares (modified from Jones 1968). The cover-board was placed over the nest bowl and from a height of 1.5 m, and the number of squares covering > 50% were recorded. Visual obstruction (VISOB) at nest sites was measured using a 1.5 m cover pole demarcated by decimeter bands (Robel et al. 1970). The pole was placed at the nest bowl and the number of increments covered were recorded along each transect from 2.5, 5, and 10 m and at a height of 0.5 and 1.5 m to simulate the view of potential nest predators. Measurements read at 5.0 m were correlated to those measured at 2.5 m and thus eliminated from further analysis ($r^2 = 0.67 - 0.84$, $P < 0.001$).

I recorded physical macrohabitat characteristics at all sites. These were slope, aspect, elevation, and cover type. Cover type, as delineated by Colorado Gap was shrub steppe (sage brush), mountain shrub, CRP, riparian, grassland or agricultural field (Colorado Gap Analysis Project 2001). Agricultural fields consisted of either wheat or hay fields. Species richness was estimated by counting the number of forb and grass species present in the microplots. Additionally, distance to nearest anthill, visible roadway, telephone pole, power line, and fence post was estimated using a range finder.

There were 156 plant species identified at nest and random sites over the 2 years of study (Appendix 1-A). Thus, analyzing cover by individual plant species was not feasible compared to the number of plots sampled. Instead, I summarized individual plant species by their frequency of occurrence within each plot and ranked them by their abundance within nest and random locations.

Specific Methods

Reproduction.

Nest initiation was compared between years and between ages of hens using a chi-squared goodness of fit test. Nest success was compared between years, ages of hens and location using a chi-squared goodness of fit test (Ott and Longnecker 2001). Clutch initiation date and clutch size between ages and years were compared using ANOVA (Ott and Longnecker 2001).

Vegetation sampling.

I partitioned the variables of slope, aspect, elevation, distance to nearest structure, distance to nearest 2-track and distance to nearest anthill into categories. The categories for slope were partitioned into 3 categories (0-5°, 6-10°, > 10°). Aspect was partitioned into 5

categories: 0° (no aspect), 315-45° (northerly), 46-135° (easterly), 136-225° (southerly) and 226-314° (westerly). Elevation was characterized as low (< 2,020 m), medium (2,021-2,140 m) and high (> 2,141 m). Distances to nearest visible structure and nearest 2-track were categorized as 0-100 m, 101-200 m, and > 200 m. Distance to nearest anthill was partitioned into 3 classifications (0-25 m, 26-50 m, > 50 m). Prior to examination, variables were assessed for correlation strength (Ott and Longnecker 2001). I used chi-squared tests to determine whether there were differences in macrohabitat between years and for successful and unsuccessful nests.

Vegetation variables were divided into 2 groups, those measured at the nest bowl and those measured in the surrounding area (2.5, 5, and 10 m). Grass height measurements were summarized at 0 and 1 m. Means of cover estimates were obtained by using the mid-point value of each cover class. Variables were assessed for normality and transformed when necessary. I used a multivariate analysis of variance (MANOVA) to assess microhabitat variables at random locations between years, locations (Axial Basin or Danforth Hills) and the year*location interaction. Canonical variables were used to assess for multicollinearity. Microhabitat variables that varied between years were assessed for correlation strength and then entered in a forward step-wise logistic regression with the principle components and the class variable year. A principal components analysis (PCA) was conducted on the random locations to reduce the amount of variables by combining highly correlated variables (Johnson and Wichern 2002). Nest sites were scored with the principal components generated from the pooled random plots. Forward step-wise logistic regression was used to model the importance of habitat variables in predicting each of 2 binary variables; nest or random and successful or non-successful nests (Beier 1989). A significance level of $P \leq 0.10$

was used to determine which variables entered and remained in the model. This analysis was performed in SAS 8.2 (SAS Institute 1999).

RESULTS

Reproductive Rates

Nest initiation rates for 2001 (86%, $n = 50$) were similar ($\chi^2 = 42$, $P = 0.518$) to those reported in 2002 (90%, $n = 69$), therefore years were pooled to compare between ages. The nest initiation rate for adults and yearlings was 92% ($n = 85$) and 79% ($n = 34$), respectively ($\chi^2 = 3.57$, $P = 0.059$). Nest success for 2001 and 2002 was 64%, $n = 42$ and 49%, $n = 65$, respectively ($\chi^2 = 2.34$, $P = 0.130$) (Table 1.1). Years were pooled for comparison between ages and locations. Nest success for adults (58%, $n = 81$) did not differ ($\chi^2 = 1.12$, $P = 0.292$) from that of yearlings (46%, $n = 26$). Nest success for individuals in the Axial Basin (54%, $n = 53$) was not different ($\chi^2 = 0.53$, $P = 0.473$) than that of individuals in the Danforth Hills (61%, $n = 41$). In 2001, only 1 female of 12 who lost their clutch attempted to renest and was successful. In 2002, 3 hens of 20 attempted to renest, 2 were successful. Hen success over both years was 57% ($n = 103$).

Mean clutch initiation date for 2001 was 26 April ($SE = 1.76$, $n = 25$). Mean clutch initiation date for 2002 was 21 April ($SE = 0.91$, $n = 51$), 5 days earlier ($F = 4.74$, $P = 0.033$) than that of 2001. Mean clutch initiation date did not differ ($F = 2.08$, $P = 0.154$) for adult (22 April, $n = 58$) and yearling females (25 April, $n = 19$). Average clutch size for 2001 ($n = 39$) and 2002 ($n = 42$) was equal at 6.67, $SE = 0.25$ ($F = 0.49$, $P = 0.484$). Mean clutch size for adult females (7.04, $SE = 0.20$, $n = 59$) was larger ($F = 13.81$, $P < 0.001$) than that of yearlings (5.68, $SE = 0.29$, $n = 22$).

Nest Predators

Of the depredated nests ($n = 40$) over both years, 70% ($n = 28$) were attributed to mammalian predators, 5% ($n = 2$) avian, and 25% ($n = 10$) unknown (Table 1.2). One female abandoned her nest in 2001, while in 2002, 4 females abandoned nests. The nests depredated by avian suspects exhibited no nest material displacement and shells remained in the nest or were dispersed vertically. Eggs exhibited small openings in the side and had conspicuous yolk. Of the suspected mammalian depredations, none showed aerial dispersal and 91% showed ground dispersal of nest material. Of those, 36% exhibited 26-50% of nest material displacement and 23% exhibited 51-75% displacement. Thirteen percent of suspected mammalian predators cached 1-3 eggs outside of the nest under > 3 cm of soil. Seventy-seven percent of suspected mammalian depredations showed some digging at the nest site. The mean number of dig sites was 1.8, and 53% were 11-20 cm, 24% were > 20 cm, 18% were 6-10 cm, and 6% were 1-5 cm in width. There was > 1 shell found at 86% of mammalian-suspected nest depredations. Of these, 18% had small holes so that $> \frac{3}{4}$ of the shell was intact and 60% had large holes so that $\frac{1}{2}$ to $\frac{3}{4}$ of the shell was still intact. The remaining eggs had $< \frac{1}{2}$ eggshell intact. The location of these openings in eggshells were sometimes mixed within a nest. Of 73 eggs, 73% of openings were on the side, 19% were on the side-end and 8% were on the end. Seventy-five percent of eggs were clean and 25% had conspicuous yolk remaining in the shell ($n = 89$). Hair samples were found at 3 nest depredation sites and 10 females were killed while incubating. Of the nests abandoned, 2 were due to researcher monitoring and 1 female abandoned immediately following the passage of a flock of sheep accompanied by sheep dogs. The reason for abandonment of the remaining nests is unknown.

Vegetation Sampling

Macrohabitat.

Of the 94 known nest sites, 90% ($n = 85$) occurred in a sage-steppe community, 5% ($n = 5$) in mountain shrub, 3% ($n = 3$) in CRP and 1% ($n = 1$) in a wheat field. No differences were detected among relative physical macrohabitat characteristics between years at random sites ($P > 0.128$) and so data were pooled (Table 1.3). There were no differences between proportion of use of physical macrohabitat characteristics measured at successful and non-successful nests (Table 1.4). There were no differences between relative use at random and nest sites except that nest sites tended to fall within the closest category (< 25 m) to the nearest anthill at a greater proportion ($\chi^2 = 8.44$, 3 *df*, $P = 0.038$, $n = 159$) than at random sites (32 vs. 14%) (Table 1.4).

Microhabitat.

A difference was found between microhabitat characteristics at random sites for location* year (Wilk's $\lambda = 0.49$; $F = 1.89$; 25,45 *df*; $P = 0.031$), location (Wilk's $\lambda = 0.46$; $F = 2.11$, 25,45 *df*; $P = 0.014$) and years (Wilk's $\lambda = 0.30$; $F = 4.12$, 25,45 *df*; $P < 0.001$). Assessment of the canonical coefficients revealed multicollinearity, thus the structural coefficients were used to assess which variables contributed to overall differences. The interaction, location*year was ordinal, and therefore I was able to interpret the main effects (Johnson and Wichern 2002). The habitat variables contributing to this difference included percent shrub cover ($F = 6.9$, $P = 0.011$), forb cover at the intersection ($F = 12.27$, $P = 0.001$), grass cover at the intersection ($F = 7.10$, $P = 0.100$), average grass cover ($F = 4.76$, $P = 0.033$) and visual obstruction between 0.5-1.0 m read from 0.5 m height and a distance of

10 m ($F = 4.56$, $P = 0.042$). The herbaceous components contributing to this difference were accentuated in the Axial Basin due to the drought condition in 2002.

The habitat variables that differed from the Axial Basin and Danforth Hills at the intersection were shrub height, grass height, percent litter and percent bare ground. Additionally, percent sagebrush cover, percent forb cover, percent bare ground and percent litter averaged over the plot, species richness and 6 visual obstruction differed between locations (Table 1.5). The habitat characteristics that varied between years at random locations were species richness, cover board reading, grass height at the intersection, grass height at 1 m, and VISOB > 50cm from 10.0 m and a reading height of 0.5 m (Table 1.6). None of these variables were highly correlated ($r^2 \leq 0.34$). A PCA of 75 random sites minus the above 5 variables produced a description of the structural habitat gradients within the study area. With 21 structural variables, the PCA defined 5 principal components, accounting for 78% of the overall variance. Each of the principal components considered had an Eigenvalue > 1 (Table 1.7).

The 5 principal components retained for further analysis each described an ecologically interpretable gradient. The first component was defined by cover at the intersection and was accompanied by shrub height at 0 m and visual obstruction readings. The second component varied along a gradient of ground cover with litter and exotics on the negative end of the scale and bare ground on the positive end. The third principal component was defined by a gradient of grass cover with grass and bare ground cover on the positive end and litter on the negative end. The fourth component described a complex gradient of structure with the scale ranging from herbaceous cover to tall shrubs, a high proportion of shrub cover, sagebrush, and a high percent of exotics. This addressed the overall

physiognomy of the sage-steppe community. Principal component 5 was characterized by the understory component and involved the forb and grass components of the community (Table 1.7).

Logistic regression with forward step-wise entry found PC 1, PC 5, grass height at 0 m and VISOBa23 to be significant predictors of nest occurrence (Table 1.8). Variables of importance within PC 1 included shrub cover, shrub height at 0 m, and visual obstruction readings (Table 1.7). Grass and forb cover were the main components of PC 5. The logistic regression equation was $\text{Logit}(Y) = 1.0 + 0.9(\text{PC } 1) - 0.6(\text{PC } 5) - 0.08(\text{GHEIGHT0}) - 0.7(\text{VISOBa23}) + e$. Nest shrub height and all visual obstruction readings were higher at nest sites than at random (Table 1.9). Mean percent shrub cover was 34% at nest sites and 24% at random sites. Forb cover was greater at nest sites than random and the alternative was found for grass cover. Grass height at 0 m was 13.8 cm at nest sites and 15.5 cm at random sites (Table 1.9).

Logistic regression was also used to predict nest success. The habitat variables that entered the model as significant predictors of nest success were PC 5 and grass height measured at 0 and 1 m (Table 1.8). The logistic regression equation was $\text{Logit}(Y) = -1.5 + 0.5(\text{PC } 5) + 0.1(\text{GHEIGHT0}) + 0.1(\text{GHEIGHT1}) + e$. Variables of importance within PC 5 were grass and forb cover (Table 1.7). Forb cover was greater at the nest bowl and within the plot site for successful nests (Table 1.9). Average grass cover was greater over the plot for successful nests. Mean grass heights measured at 0 and 1 m were 11.7 cm and 13.5 cm for unsuccessful nests and 15.4 cm and 18.2 cm for successful nests.

Individual Plant Frequency.

Because the MANOVA indicated that there were no differences among percent forbs or grasses between years, I pooled plant frequency data. Of 94 nest sites, only 2 occurred under a shrub species other than sagebrush. One female nested under a rubber rabbitbrush (*Ericameria nauseosa*), and 1 nested under a Russian thistle (*Salsola iberica*). Both were successful. Shrub species that occurred at > 60 % of nest and random sites were sagebrush and dead sagebrush (Figure 1.1). Forbs found in > 60% of plots included clover (*Trifolium* spp.), pale madwort (*Alyssum alyssoides*), longleaf phlox (*Phlox longifolia*), maiden blue eyed Mary (*Collinsia parviflora*), false dandelion (*Agoseris glauca*) and lupine (*Lupinus sericeus*). Grasses that occurred in > 60 % of nest sites included western wheatgrass (*Pascopyron smithii*) and cheat grass (*Bromus tectorum*). Greater species occurrence at nest sites may indicate selection for these species. Females may be selecting false dandelion, lupine, and salt and pepper parsley (*Lomatium orientale*) and avoiding copper mallow (*Sphaeralcea coccinea*) (Figure 1.1).

DISCUSSION

Reproductive Rates

Nest initiation rates for adult and yearling females were 92% and 79%, respectively. Although this was not statistically significant it verifies previous reports which indicate adults have a higher nest initiation rate than yearlings (Bergerud 1988, Connelly et al. 1993). While Connelly et al. (1993) reported initiation rates of 78% for adults and 55% for yearlings in southeast Idaho, my results are similar to those reported in Washington by Sveum (1995) of 80% ($n = 95$) and Schroeder (1997) who observed 100% ($n = 129$). I believe my nest

initiation rates may be biased low because insufficient monitoring could potentially have missed some nesting efforts.

Clutch initiation dates ranged from 8 April to 20 May. Renesting efforts ranged from 15 May to 25 May. These are earlier than nesting dates reported for North Park, Colorado, which were between 21 April and 21 June (Dargon and Keller 1940). Braun (1981) reported peak hatching dates in southern Moffat County from 15-21 June. Peak hatch dates in the Axial Basin and Danforth Hills occurred from 17-26 May. Peak hatch dates were earlier than reported by Braun (1981) indicating that I did not miss many initial nesting efforts. Clutch initiation dates were earlier in 2002 likely due to drier conditions and a milder winter. Regional climate maps for northwest Colorado showed that there was a 21.3 cm decrease in precipitation from 2001 to 2002 for April to June and a + 3°C departure of average temperature for June 2002 (Appendix 1-B). Additionally, December – February 2002 received 25-50% of normal precipitation (NOAA 2003).

Mean clutch size in the Axial Basin (6.67) was smaller than previous studies in Colorado, which reported clutch sizes of 7.5 ($n = 69$) (Keller et al. 1941) and 7.0 ($n = 29$) (Peterson 1980). Adults laid larger clutches but had similar nest success to yearlings. Commonly, adult clutch sizes are 0.2-2.1 eggs greater than yearlings (Schroeder et al. 1999). Connelly et al. (1994) also found nest success to be similar between ages. Combined nest success for yearling and adult females over 2 years in Axial Basin was 55% ($n = 107$). My values are normal to high in comparison with other Colorado studies, which range between 25% (Carr 1967) and 58% (Peterson 1980), similar to results in Idaho (52%, $n = 166$), and high compared to nest success rates in Oregon (14.5-30%) and Washington (36.7-40.9%) (Schroeder et al. 1999). Renesting effort was restricted to 4 females over 2 years.

The Axial Basin was characterized by habitat with less species richness, sagebrush, forb and litter cover and more bare ground than in the Danforth Hills (Table 1.5). Land in the privately-owned Danforth Hills is grazed by livestock, while the Axial Basin consists of a patchwork of private, BLM and state lands, and is used for grazing, crops and CRP. The dry winter and spring in 2002 exacerbated herbaceous habitat conditions in the Axial Basin, an effect not observed in the Danforth Hills. Habitat restrictions in the Axial Basin may have caused females to move further to nest sites and increase their brood home ranges (Chapter 4).

Altitudinal differences, soil types, wildlife and livestock grazing may be factors influencing the vegetation characteristics in the 2 locations. Elevation ranges from 1,818 – 2,000 m in the Axial Basin and from 2,001 – 2,388 m in the Danforth Hills. Large numbers of elk winter in the Axial Basin and their influence on vegetation was unmeasured. The grazing regime as it exists now in the Danforth Hills consists of cattle and sheep rotated through pastures from mid May until October. Total area of these allotments is 51,696 ha. The grazing regime in the Axial Basin, as per BLM data, includes sheep, cattle and horses, and grazing occurs on a total of 35,938 ha of private, federal and state lands. Utilization occurs year-round on most allotments. Laycock (1979) indicated that a high level of spring grazing by cattle and sheep in a sage-steppe community reduces the vigor and production of herbaceous species. Grazing can move the sage-steppe community into a lower successional state with a diminished herbaceous understory (Laycock 1991). Wild and domestic ungulate grazing would add to this impact. The combination of abiotic factors coupled with large ungulate grazing and livestock grazing may contribute to the differences between habitat characteristics in the Axial Basin and Danforth Hills.

Nest Predators

Potential nest predators in Moffat County include badgers (*Taxidea taxus*), Richardson's ground squirrels (*Citellus richardsoni*), common ravens (*Corvus corax*), American crows (*Corvus brachyrhynchos*), black-billed magpies (*Pica hudsonia*), coyotes (*Canis latrans*), weasels (*Mustela* sp.), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), porcupine (*Erethizon dorsatum*) and gulls (*Larus* sp.). Interpreting cause-specific nest depredation from egg and nest remains can be confounded due to inter-specific overlap and intra-specific variation in nest destruction, stage of development, researcher experience, partial nest depredation, scavenging and parental activity at depredated nests (Larivière 1999). Thus, despite inferring only mammalian or avian predation, my results should be viewed cautiously. Seventy percent of depredated nests in the Axial Basin and Danforth Hills were attributed to mammalian predators, although species specific nest depredations could not be estimated from available data. This was consistent with data from North Park, Jackson County, Colorado where badgers and ground squirrels caused the majority of nest depredations (Gill 1964). Common ravens and coyotes preyed upon 76% of nests ($n = 21$) in Wyoming (Allred 1942). Autenrieth (1981) determined common ravens to be the most important nest predator in Idaho. Similarly, in Oregon, common ravens accounted for 66% of 131 depredated nests (Batterson and Morse 1948). Avian predators in the Axial Basin and Danforth Hills accounted for only 5% of destroyed nests.

Vegetation Sampling

The only macrohabitat characteristics to vary between random and nest sites was distance to nearest anthill. This may suggest that greater sage-grouse are selecting nest sites with close proximity to anthills in order to provide early sustenance for chicks. Insects

dominate the diet of chicks in their first 2 weeks, and ants (Hymenoptera) may provide a consistent food resource (Knowlton and Thornley 1942, Klebenow and Gray 1968, Drut et al. 1994). No macrohabitat differences existed between successful and unsuccessful nests. These results may be due to little habitat diversity within the physiographic characteristics at my study sites (Porter and Church 1987, Åberg et al. 2000).

Despite the apparent homogeneity of the shrub-steppe community in my study area, selection was apparent at the microhabitat scale. Greater sage-grouse females in the Axial Basin and Danforth Hills selected nest sites with greater shrub cover, greater shrub height and greater grass and forb cover than random sites. Klebenow (1969) noted that nest sites were generally under shrubs with more ground, lateral, and shrub cover than at random sites. Bowman and Harris (1980) indicated canopy cover strongly influenced prey vulnerability. Successful nests tended to be found in areas of higher canopy cover ($\geq 15\%$) than unsuccessful nests (Klebenow 1969, Wallestad and Pyrah 1974, Gregg et al. 1994). In North Park, Colorado, nest cover averaged 44% ($n = 19$) (Schoenberg 1982). Additionally, medium height shrubs (30-70 cm) have been deemed important for nest success (Wallestad and Pyrah 1974, Schoenberg 1982, Gregg et al. 1994, Delong et al. 1995, Connelly et al. 2000). Females in the study area selected nest sites that were characterized by a mean shrub height of 56.5 cm and nest shrub height of 79.4 cm. Percent grass and forb cover was also greater at nest sites than at random. Grass height was also selected as a predictor of nest occurrence and was greater at random locations than at nest sites. The difference, however, was < 2 cm and may not be biologically significant.

Guidelines for protection of greater sage-grouse breeding habitats suggest 15-35% canopy cover of sagebrush and perennial herbaceous cover averaging ≥ 18 cm in height and a

diversity of forbs (Connelly et al. 2000). Mean canopy cover of sagebrush at random sites in the Axial Basin and Danforth Hills was 17%, suggesting that the study site has appropriate canopy cover within the sage-steppe community. Grass height at the nest bowl and at 1 m were variables that predicted nest success. This is consistent with other observational studies in Oregon and Idaho. Klebenow (1969), Wakkinen (1990), Gregg et al. (1994) and Delong et al. (1995) indicated tall grass cover (≥ 18 cm) as a parameter significant for nest success. While guidelines suggest a grass height of ≥ 18 cm for nesting (Connelly et al. 2000), high nest success of 64% in 2001 and 49% in 2002 suggest that these guidelines may not be applicable to Colorado. Rather, minimum grass height, based on successful nests within the study area, should range between 15-18 cm (Table 1.9).

Apparent nest success for 2001 was greater than 2002 by 15%. Although this was not statistically significant, it may be biologically relevant. The nest habitat characteristics that varied among years were those that would have been influenced by the hotter, drier conditions in 2002 (Appendix 1-B). Species richness, cover board readings, grass height at the intersection of the transects and at 1 m, and visual obstruction readings were all lower in 2002 than 2001 (Table 1.6). There was a reduction of 5-7 cm in grass height between 2001 and 2002 and visual obstruction at the intersection was lower in 2002. These are likely reasons that nest success was lower in 2002 and suggests that grass height, although not limiting the population in years with high precipitation may be an important element limiting nest success in drought years.

Preference for individual plant species was apparent for forbs such as false dandelion, lupine, and salt and pepper parsley. These species may be selected for their structural characteristics; particularly lupine which ranges from 50-100 cm tall (Kershaw et al. 1998).

Similarly, Apa (1998) found the family Leguminosae, which includes lupine, to be critical in the classification of greater sage-grouse nest sites from random sites in Idaho. False dandelion was found in the crops of greater sage-grouse carcasses in the study site as a forage item. Salt and pepper parsley may provide cover at nest sites. Globe mallow was avoided at nest sites, perhaps because this plant occupies dry, open habitat types (Kershaw et al. 1998).

MANAGEMENT IMPLICATIONS

There is concern over decreasing greater sage-grouse populations throughout their range. Causes are frequently attributed to habitat alteration due to habitat fragmentation, land conversion, overgrazing, introduction of exotic weeds, pesticides and altered fire regimes (Miller and Eddleman 2000). My results indicated the importance of shrub cover, native herbaceous cover, and grass height on nest success. Successful nests in the study site featured grass heights of 15 cm and 18 cm at the nest bowl and at 1 m from the nest bowl, respectively. Current habitat guidelines suggest grass heights be maintained at ≥ 18 cm. However, given the normal to high nest success in the population, grass heights of 15-18 cm may be adequate. Nest success in the study site varied by year, as did visual obstruction and grass height, which illustrates the interaction of these habitat components. Management actions should maintain native forb and grass communities as well as the shrub component in the sage-steppe community.

The Axial Basin compared to the Danforth Hills has less shrub cover, visual obstruction, forb cover over the nest plot and grass height at 0 m, all variables deemed important for nest site selection and success. Difference between the 2 areas may be due to elevation, soil type, wildlife grazing and the timing and intensity of livestock grazing. A

large-scale, controlled grazing study that also evaluates the impact of elk foraging in winter could determine what may be influencing differences in habitat characteristics between the Axial Basin and Danforth Hills.

While Beck and Mitchell (2000) stated that livestock grazing tends to be the most detrimental to greater sage-grouse during their nesting activities, nest success did not differ between locations with different grazing regimes in my study. Because of the importance of leks to breeding greater sage-grouse, I recommend that leks not be used as feeding sites for sheep during the breeding season (mid-March to mid-April).

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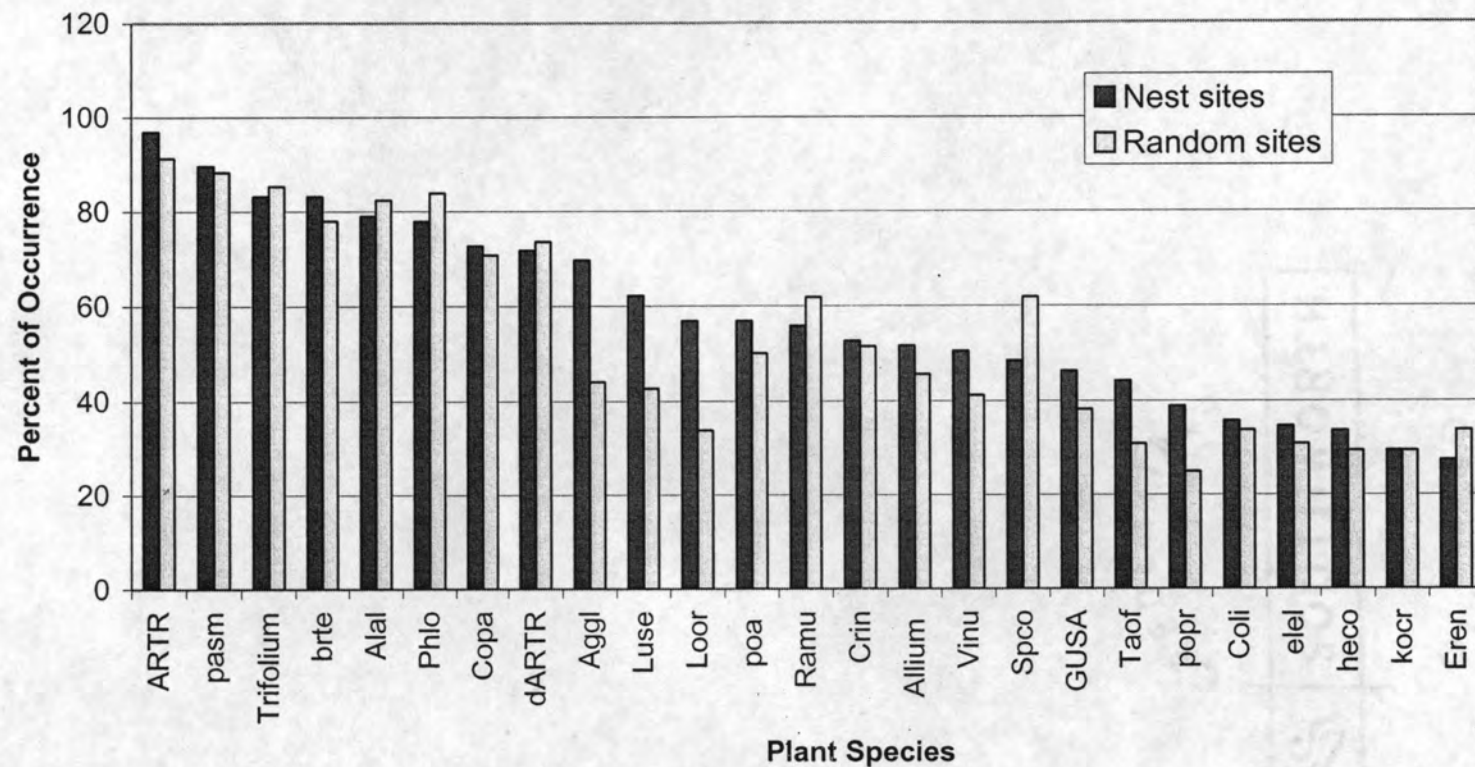


Figure 1.1. The 25 of the most commonly plant species at greater sage-grouse nest and random sites in Axial Basin and Danforth Hills, Colorado, 2001 and 2002. Shrubs are 4-letter genus/species code in capitals, grasses are 4-letter genus/species codes in all lower case, and forbs are 4-letter genus/species code with the first letter capitalized. Scientific names, common names and native status are found in Appendix 1-A.

Table 1.1. Number of nests and female greater sage-grouse and their nest fate in northwest Colorado, 2001/2002.

	Nests		Females	
	Successful	Unsuccessful	Successful	Unsuccessful
Year				
2001	27	15	27	14
2002	32	33	32	32
Total	59	48	59	45
Age				
Adult	47	34	47	31
Yearling	12	14	12	14
Total	59	48	59	45

Table 1.2. Cause-specific nest fate of radio-marked greater sage-grouse females in northwest Colorado, 2001/2002.

Year	Successful		Depredated		Other
		Mammalian	Avian	Unknown	Abandoned
2001	30	10	1	2	1
2002	30	18	1	8	4

Table 1.3. Differences in macrohabitat characteristics (mean and standard error) between years at random sites in the Axial Basin and Danforth Hills, Colorado, 2001/2002.

Habitat Variable	2001 (n = 53)	2002 (n = 49)	χ^2	df	P-value
Slope (°)	4.9 (0.4)	7.3 (1.0)	12.8	3	0.802
Aspect (°)	172.7 (16.1)	188.6 (17.0)	78.8	4	0.361
Elevation (m)	2032 (16)	2061 (18)	84.0	3	0.449
Distance to nearest structure (m)	216.5 (43.7)	193.6 (33.5)	37.0	3	0.288
Distance to nearest 2-track (m)	166.1 (23.7)	162.1 (25.4)	52.5	3	0.128
Distance to nearest anthill *	2.6 (0.1)	2.6 (0.2)	0.7	3	0.853

* Categorical data only (1 = 0-25 m, 2 = 26-50 m, 3 > 51 m)

Table 1.4. Means and standard errors of macrohabitat characteristics and results of chi-squared tests for successful and non-successful greater sage-grouse nest sites and random sites in Axial Basin and Danforth Hills, Colorado, 2001/2002.

Habitat Variable	Random (n=93)	Nests (n=100)	P-value	Successful (n=50)	Unsuccessful (n=42)	P-value
Slope	6.0 (0.5)	5.2 (0.5)	0.441	5.4 (0.6)	4.7 (0.7)	0.685
Aspect	180 (11)	208 (12)	0.075	202 (16)	201 (19.0)	0.988
Elevation	2046 (12)	2045 (10)	0.775	2045 (13)	2040 (16)	0.442
Distance to nearest visible structure	206.7 (29.7)	205.1 (36.7)	0.290	237.2 (66.9)	184.4 (39.1)	0.496
Distance to nearest 2-track	164.3 (17.2)	146.0 (14.1)	0.189	155.6 (20.6)	129.7 (20.2)	0.538
Distance to nearest ant-hill*	2.3 (0.1)	2.6 (0.1)	0.038	2.3 (0.1)	2.3 (0.1)	0.870

* Categorical data only

Table 1.5. Microhabitat characteristics varying between locations at random sites (mean and standard error) in Moffat County, Colorado 2001/2002. ANOVA P-values are reported.

Habitat variable	Axial Basin (n=41)	Danforth Hills (n=32)	F-value	P-value
Species richness	15.1 (0.6)	18.1 (0.7)	8.98	0.004
Cover board	12.2 (1.4)	14.3 (1.5)	1.49	0.226
Percent shrub cover ^a	19.7 (2.2)	29.4 (2.8)	2.86	0.095
Percent sagebrush cover ^a	23.2 (1.7)	31.7 (2.1)	9.82	0.002
Intersection shrub height	40.7 (5.0)	62.2 (6.9)	5.44	0.023
Average shrub height	45.7 (4.1)	58.1 (5.1)	2.39	0.127
Grass height 0m	13.2 (0.9)	18.6 (2.0)	18.17	<0.001
Grass height 1m	14.6 (0.8)	16.1 (1.6)	1.27	0.263
Percent forb cover at 0 m ^a	4.7 (0.9)	8.7 (1.3)	1.95	0.167
Average forb cover ^a	4.4 (0.5)	8.1 (1.0)	7.63	0.007
Percent grass cover at 0 m ^a	4.8 (0.8)	8.5 (2.8)	0.51	0.478
Average grass cover ^a	4.8 (0.6)	7.9 (2.0)	1.21	0.275
Percent exotic cover at 0 m ^a	31.0 (4.1)	34.4 (4.6)	0.01	0.918
Average exotic cover ^a	32.6 (3.3)	27.3 (3.1)	1.17	0.283
Percent bare ground 0 m ^a	28.5 (4.8)	17.8 (4.7)	3.81	0.055
Average bare ground ^a	28.0 (3.8)	17.5 (3.1)	5.35	0.024
Percent litter cover 0 m ^a	70.5 (4.6)	79.5 (4.6)	3.93	0.051
Average litter cover ^a	72.5 (3.6)	80.2 (2.9)	3.76	0.056
VISOBa11 ^b	11.7 (2.3)	20.9 (3.0)	4.46	0.038
VISOBa13 ^b	26.4 (2.6)	37.7 (2.6)	4.39	0.040
VISOBa21 ^b	3.2 (1.4)	7.3 (1.9)	2.38	0.128
VISOBa23 ^b	8.9 (1.9)	21.9 (3.0)	9.07	0.004
VISOBb11 ^b	8.5 (1.8)	16.9 (2.9)	5.58	0.021
VISOBb13 ^b	19.1 (2.2)	30.3 (2.7)	6.91	0.011
VISOBb21 ^b	2.1 (1.3)	4.9 (1.8)	1.84	0.179
VISOBb23 ^b	4.6 (1.4)	11.6 (2.2)	4.77	0.032

^a Arcsin transformed for MANOVA, untransformed mean and SE are reported.

^b Visual obstruction readings where the letter responds to reading height (a = 0.5m, b = 1.5 m), the first number responds to the 50cm demarcations on the pole (1 = 0 m- 0.5 m, 2 = 0.5 m- 1.0 m) and the second number responds to reading distance from the pole (1 = 2.5 m, 2 = 5.0 m, 3 = 10 m).

Table 1.6. Microhabitat characteristics varying between years at random sites (mean and standard error) in northwest Colorado, 2001/2002. ANOVA P-values are reported.

Habitat variable	2001	2002	F-value	P-value
Species richness	18.0 (0.7)	15.9 (0.7)	6.76	0.011
Cover board reading	18.4 (1.3)	10.2 (1.2)	15.7	< 0.001
Grass height at intersection (cm)	20.8 (1.4)	13.8 (0.9)	13.12	0.001
Grass height at 1 m (cm)	18.9 (2.5)	13.4 (1.0)	7.47	0.008
VISOB >50 cm from 10.0 m and a reading height of 0.5 m (cm)	18.3 (1.2)	5.6 (1.6)	5.21	0.026

Table 1.7. Pattern of 5 Principal Components derived from analysis of 21 microhabitat variables from 75 random plots in Axial Basin and Danforth Hills, Colorado, 2001/2002.

Structural Feature	PC1	PC2	PC3	PC4	PC5
Percent shrub cover	0.237			0.325	
Percent sagebrush cover				0.305	
Shrub height at 0 m	0.249				
Average shrub height				0.348	
Forb cover at 0 m				-0.228	0.546
Average forb cover				-0.220	0.525
Grass cover at 0 m			0.309		0.375
Average grass cover			0.312		0.280
Exotic herbaceous cover at 0 m				0.505	
Average exotic herbaceous cover		-0.302		0.392	
Bare ground 0 m	-0.151	0.388			
Average bare ground	-0.166	0.328	0.323		
Litter 0 m		-0.385			
Average litter		-0.337	-0.319		
VISOB 0.5 m from 2.5 m 0-50 cm	0.310				
VISOB 0.5 m from 10 m 0-50 cm	0.313				
VISOB 0.5 m from 2.5 m 0.5-1 m	0.287				-0.202
VISOB 1.5 m from 2.5 m 0-0.5 m	0.306				
VISOB 1.5 m from 10 m 0-0.5 m	0.330				
VISOB 1.5 m from 2.5 m 0.5-1 m	0.257				-0.218
VISOB 1.5 m from 10 m 0.5-1 m	0.295				
Eigenvalue	7.1	3.2	2.9	1.8	1.5
Percent of variation explained	33.7	15.3	13.7	8.5	7.2
Cumulative percent	33.7	49.0	62.7	71.1	78.4

Table 1.8. Logistic regression models of habitat variables predicting the binary variables for random and nest sites or successful and unsuccessful nests of greater sage-grouse in northwest Colorado 2001/2002.

Dependant Variable	Parameters	Regression Coefficient (SE)	Wald χ^2	df	P
Random/ Nest sites	PC 1	0.913 (0.160)	32.77	1	<0.001
	PC 5	-0.563 (0.167)	11.36	1	0.001
	Grass height 0 m	-0.080 (0.033)	5.89	1	0.015
	Visual obstruction 0.5-1.0 m read from a height of 0.5 m and a distance 10 m	-0.656 (0.213)	9.50	1	0.002
Successful/ Unsuccessful nests	PC 5	0.547 (0.237)	5.34	1	0.021
	Grass height 0 m	0.069 (0.042)	2.71	1	0.100
	Grass height 1 m	0.087 (0.038)	4.40	1	0.022

Table 1.9. Mean and standard error (SE) for habitat variables measured at successful, unsuccessful, and random nest sites of greater sage-grouse in Moffat County, Colorado 2001/2002.

Variable	Total nests (n=93)	Successful (n=53)	Unsuccessful (n=40)	Random nests (n=75)
Species richness	18.9 (0.6)	19.9 (0.8)	17.6 (0.7)	16.6 (0.5)
Cover board	17.7 (0.7)	18.6 (1.0)	16.5 (1.1)	12.9 (1.0)
Percent shrub cover ^a	34.1 (1.4)	33.9 (1.9)	34.2 (2.2)	24.0 (1.8)
Percent sagebrush cover ^a	26.9 (1.4)	25.6 (1.7)	28.6 (2.2)	16.6 (1.5)
Nest shrub height	79.4 (2.5)	78.7 (3.2)	80.4 (4.0)	50.1 (4.2)
Average shrub height	56.5 (2.2)	55.7 (3.1)	57.5 (2.9)	51.1 (3.2)
Grass height 0 m	13.8 (0.7)	15.4 (0.9)	11.7 (0.9)	15.5 (1.0)
Grass height 1 m	16.2 (0.8)	18.2 (1.1)	13.5 (1.0)	15.0 (0.8)
Percent forb cover at 0 m ^a	6.9 (0.8)	7.7 (1.4)	5.8 (0.7)	6.3 (0.8)
Average forb cover ^a	8.4 (0.7)	9.3 (1.0)	7.2 (0.9)	6.2 (0.6)
Percent grass cover at 0 m ^a	3.7 (0.4)	3.7 (0.6)	3.8 (0.7)	6.4 (1.3)
Average grass cover ^a	4.4 (0.3)	4.8 (0.6)	3.9 (0.4)	6.1 (0.9)
Percent herbaceous exotic cover at 0 m ^a	30.5 (2.7)	30.5 (3.2)	30.5 (4.6)	31.9 (3.0)
Average herbaceous exotic cover ^a	29.3 (2.2)	28.6 (2.9)	30.2 (3.4)	29.5 (2.3)
Percent bare ground 0 m ^a	4.9 (1.1)	6.1 (1.8)	3.5 (0.8)	23.3 (3.3)
Average bare ground ^a	17.4 (1.6)	17.5 (2.1)	17.3 (2.5)	23.7 (2.6)
Percent litter cover 0 m ^a	87.9 (1.8)	87.7 (2.6)	88.3 (2.3)	74.9 (3.2)
Average litter cover ^a	77.5 (2.0)	78.5 (2.5)	76.2 (3.3)	75.5 (2.4)
VISOBa11 ^b	38.4 (1.0)	39.0 (1.2)	37.7 (1.8)	15.7 (1.9)
VISOBa13 ^b	46.8 (0.6)	47.4 (0.7)	46.1 (1.1)	31.5 (1.9)
VISOBa21 ^b	13.5 (1.3)	13.4 (1.7)	13.6 (1.9)	4.8 (1.1)
VISOBa23 ^b	24.6 (1.6)	23.8 (2.0)	25.8 (2.5)	14.6 (1.8)
VISOBb11 ^b	33.2 (1.2)	32.6 (1.6)	34.0 (1.7)	12.2 (1.6)
VISOBb13 ^b	40.5 (1.0)	40.8 (1.2)	40.1 (1.6)	24.1 (1.7)
VISOBb21 ^b	9.4 (1.1)	9.0 (1.4)	10.0 (1.7)	3.2 (1.0)
VISOBb23 ^b	15.9 (1.3)	14.9 (1.7)	17.3 (2.1)	7.5 (1.3)

^a Arcsin transformed for MANOVA, untransformed mean and SE are reported

^b Visual obstruction readings where the letter responds to reading height (a = 0.5m, b = 1.5 m), the first number responds to the 50cm demarcations on the pole (1 = 0 m- 0.5 m, 2 = 0.5 m- 1.0 m) and the second number responds to reading distance from the pole (1 = 2.5 m, 2 = 5.0 m, 3 = 10 m).

Appendix 1-A. Vegetation species and their native status identified at microhabitat plot sites of greater sage-grouse nests and random sites in the Axial Basin and Danforth Hills Colorado, 2001-2002. Code is the abbreviated genus and species name (first 2 letters of each). Nomenclature is taken from the PLANTS Database (USDA 2003).

Scientific name	Common Name	Code	Native Status
FORBS			
<i>Achillea millefolium</i>	Yarrow	ACMI	Native ^a
<i>Agoseris glauca</i>	False dandelion	AGGL	Native ^a
<i>Allium</i> spp.	Wild onion (genus only)		Native ^a
<i>Alysum alyssoides</i>	Pale madwort	ALAL	Introduced ^{1 b}
<i>Antennaria</i> spp.	Pussytoes (genus only)		Native ^a
<i>Antennaria microphylla</i>	Littleleaf pussytoes	ANPA	Native ^a
<i>Arabis</i> spp.	Rockcress (genus only)		Native ^a
<i>Arabis drummondii</i>	Drummond's rockcress	ARDR	Native ^a
<i>Arcticum minimus</i>	Common burdock	ARMI	No record ^a
<i>Astragalus/Oxytropis</i>	Astragalus or Oxytropis	ASOX	Native ^a
<i>Astragalus</i> spp.	Locoweed (genus only)		Native ^a
<i>Astragalus purshii</i>	Woollypod milk-vetch	ASPU	Native ^a
<i>Balsamorhiza sagittata</i>	Arrow-leaved balsamroot	BASA	Native ^a
<i>Calochortus nuttallii</i>	Sego lily	CANU	Native ^a
<i>Capsella bursa-pastoris</i>	Shepards purse	CABU	Introduced ^a
<i>Cardaria draba</i>	White top	CADR	Introduced ^a
<i>Castilleja miniata</i>	Indian paintbush	CAMI	Native ^a
<i>Camelina microcarpa</i>	Smallseed falseflax	CAMIC	Introduced ^{1 b}
<i>Chenopodium</i>	Pigweed, goosefoot		Native ^a
<i>Chenopodium berlandieri</i>	Netseed lambsquarters	CHBE	Native ^a
<i>Chenopodium multifidum</i>	Cutleaf goosefoot	CHMU	Native ^a
<i>Chenopodium vulvaria</i>	Stinking goosefoot	CHVU	Introduced ^a
<i>Chorispura tenella</i>	Blue mustard	CHTE	Introduced ^{1 2 3 a b}
<i>Cicuta douglasii</i>	Douglas' water hemlock	CIDO	Native ^a
<i>Cirsium arvense</i>	Canada thistle	CIAR	Introduced ^{1 2 3 a b}
<i>Cirsium undulatum</i>	Wavyleaf thistle	CIUM	Native ^b
<i>Cirsium vulgare</i>	Bull thistle	CIVU	Introduced ^a
<i>Collinsia parviflora</i>	Maiden blue-eyed mary	COPA	Native ^a
<i>Collomia linearis</i>	Narrow leafed collomia	COLI	Native ^a
<i>Comandra umbellata</i>	Bastard toadflax	COUM	Native ^a
<i>Conium maculatum</i>	Poison hemlock	COMA	Introduced ^{1 b}
<i>Crepis intermedium</i>	Gray hawksbeard	CRIN	Native ^a
<i>Cryptantha glomerata</i>	Cryphaea moss	CRGL	Native ^a
<i>Cynoglossum officinale</i>	Hound's tongue	CYOF	Introduced ^{1 b}
<i>Delphinium bicolor</i>	Low larkspur	DEBI	Native ^a

Appendix 1-A. Continued.

Scientific name	Common Name	Code	Native Status
<i>Descurainia sophia</i>	Tansy mustard Flixweed	DESO	Introduced ^{1 3 a b}
<i>Echinocereus</i> spp.	Hedgehog cactus (genus only)		Native ^a
<i>Erysimum asperum</i>	Western wallflower	ERAS	Native ^a
<i>Erigeron engelmannii</i>	Engelmann's fleabane	EREN	Native ^a
<i>Erigeron filifolius</i>	Thread leafed daisy	ERFI	Native ^a
<i>Erigonum ovalifolium</i>	Cushion buckwheat	EROV	Native ^a
<i>Erigonum umbellatum</i>	Sulphur buckwheat	ERU M	Native ^a
<i>Euphorbia esula</i>	Leafy Spurge	EUES	Introduced ^{a 1 2}
<i>Fritillaria atropurpurea</i>	Leopard lily	FRAT	Native ^a
<i>Galium boreale</i>	Northern Bedstraw	GABO	Native ^a
<i>Gentian linearis</i>	Narrowleaf gentian	GELI	Native ^a
<i>Geranium caespitosum</i>	Common wild geranium	GECA	Native ^a
<i>Glycyrrhiza lepidota</i>	Wild Licorice	GLLE	Native ^a
<i>Grindella squarrosa</i>	Curly-cup gum weed	GRSQ	Native ^a
<i>Helianthus</i>	Sunflower		Native ^a
<i>Heterotheca villosa</i>	Golden aster	HEVI	Native ^a
<i>Huechera parvifolia</i>	Saxifrage	HUPA	No record ^a
<i>Hydrophyllum</i>	Water leaf		Native ^a
<i>Ipomea</i> spp.	Morning glory (genus only)		Introduced ^a
<i>Ipomopsis aggregata</i>	Scarlet gilia	IPAG	Native ^a
<i>Kochia scoparia</i>	Kochia	KOSC	Introduced ^{1 b}
<i>Lactuca occidentalis</i>	Bluebird sitchseed	LAOC	Native ^a
<i>Lactuca serriola</i>	Prickly lettuce	LASE	Introduced ^{1 b}
<i>Lathyrus ochroleucus</i>	Creamy peavine	LAOC	Native ^a
<i>Lepidium perfoliatum</i>	Clasping pepperweed	LEPE	Introduced ^{1 b}
<i>Linum lewisii</i>	Western Blue flax	LILE	Native ^a
<i>Linaria vulgaris</i>	Yellow toad flax	LIVU	Introduced ^{1 2 3 a b}
<i>Lithospermum ruderales</i>	Puccoon	LIRU	Native ^a
<i>Lomatium orientale</i>	Salt and pepper parsley	LOOR	Native ^a
<i>Lomatium triternatum</i>	Parsley	LOTR	Native ^a
<i>Ipomopsis aggregata</i>	Scarlet gilia	LPAG	Native ^a
<i>Lupinus minimus</i>	Cushion lupine	LUMI	Native ^a
<i>Lupinus sericeus</i>	Silky lupine	LUSE	Native ^a
<i>Lygodesmia juncea</i>	Skeletonweed	LYJU	Native ^a
<i>Machaeranthera canescens</i>	Hoary aster	MAC A	Native ^a
<i>Medicago sativa</i>	Alfalfa	MESA	Introduced ^a
<i>Melilotus officinalis</i>	Yellow sweet clover	MEOF	Introduced ^{1 2 b}
<i>Mentha spicata</i>	Spearmint	MESP	Introduced ^a
<i>Mertensia longiflora</i>	Bluebells	MELO	Native ^a

Appendix 1-A. Continued.

Scientific name	Common Name	Code	Native Status
<i>Microsteris</i>	Microsteris		No Record ^a
<i>Nemophila breviflora</i>	Nemophila	NEBR	Native ^a
<i>Onobrychis viciaefolia</i>	Sanfoin	ONVI	Introduced ^a
<i>Opuntia polyacantha</i>	Starvation cactus	OPPO	Native ^a
<i>Oxytropis sericeus</i>	Locoweed	OXSE	Native ^a
<i>Penstemon</i> spp.	Penstemon (genus only)		Native ^a
<i>Penstemon gairdneri</i>	Gardner's beardtongue	PEGA	Native ^a
<i>Phlox hoodii</i>	Phlox	PHHO	Native ^a
<i>Phlox longifolia</i>	Phlox	PHLO	Native ^a
<i>Plantago</i>	Plantain		Native ^a
<i>Plantago hookeri</i>	California plantain	PLHO	Native ^a
<i>Plantago patagonica</i>	Woolly plantain	PLPA	Native ^a
<i>Polygonum</i> spp.	Knotweed (genus only)		Native ^a
<i>Potentilla</i> spp.	Cinquefoil		Native ^a
<i>Pseudostellari jamesiana</i>	Tuber starwort	PSJA	Native ^a
<i>Ranunculus muricatus</i>	Pricklefruit buttercup	RAMU	Introduced ^{1 b}
<i>Rorippa nasturtium</i>	Watercress	RONA	Native ^a
<i>Rumex</i> spp.	Sorrel		Both ^a
<i>Salsola iberica</i>	Russian thistle	SAIB	Introduced ^{2 b}
<i>Senecia canus</i>	Woolly groundsel	SECA	Native ^a
<i>Senecio integerrimus</i>	Butterweed, Golden ragwort	SEIN	Native ^a
<i>Solidago</i> spp.	Goldenrod (genus only)		Native ^b
<i>Solanum</i> spp.	Nightshade (genus only)		No Record ^a
<i>Sphaeralcea coccinea</i>	Copper mallow	SPCO	Native ^a
<i>Taraxacum officinale</i>	Dandelion	TAOF	Introduced ^{1 b}
<i>Thlaspi arvense</i>	Field pennycress	THAR	Introduced ^{1 b}
<i>Townsendii hookeri</i>	Easter daisy	TOHO	Native ^a
<i>Tragapogan dubius</i>	Salsify	TRDU	Introduced ^{1 2b}
<i>Trifolium arvense</i>	Rabbit foot clover	TRAR	Introduced ^a
<i>Trifolium fragiferum</i>	Strawberry clover	TRFR	Introduced ^a
<i>Verbascum thapsus</i>	Common mullein	VETH	Introduced ^{1 b}
<i>Viola nuttallii</i>	Violet	VINU	Native ^a
<i>Viscia americana</i>	American vetch	VIAM	Native ^a
<i>Viscia villosa</i>	Winter vetch	VIVI	Introduced ^a
<i>Zigadenus venenosus</i>	Death camas	ZIVE	Native ^a
GRASSES			
<i>Achnatherum hymenoides</i>	Indian Rice Grass	ACHY	Native ^{a c}
<i>Aegilops cylindrical</i>	Jointed goatgrass	AECY	Introduced ^{1 a}
<i>Agropyron cristatum</i>	Crested wheatgrass	AGCR	Introduced ^{2 a}
<i>Agropyron dasystachyum</i>	Thickspike wheatgrass	AGDA	Native ^c

Appendix 1-A. Continued.

Scientific name	Common Name	Code	Native Status
<i>Agropyron griffithii</i>	Montana wheatgrass	AGGR	Native ^{a c}
<i>Agropyron intermedium</i>	Intermediate wheatgrass	AGIN	Introduced ^{1 a}
<i>Agropyron repens</i>	Quackgrass	AGRE	Introduced ^{1 2 a}
<i>Agropyron riparum</i>	Stream bank wheatgrass	AGRI	Native ^{a c}
<i>Agropyron trachycaulum</i>	Slender wheat grass	AGTRA	Native ^{a c}
<i>Agrostis stolonifera</i>	Red Top Bent	AGST	Native ^{a c}
<i>Bromus inermis</i>	Smooth brome	BRIN	Introduced ^{1 a}
<i>Bromus japonicus</i>	Japanese brome	BRJA	Introduced ^{1 2 a}
<i>Bromus marginatus</i>	Mountain brome	BRMA	Native ^{a c}
<i>Bromus tectorum</i>	Cheat grass	BRTE	Introduced ^c
<i>Carex</i> spp.	Sedge (genus only)		Native ^a
<i>Dactylis glomerata</i>	Orchard grass	DAGL	Introduced ^{1 2 a}
<i>Elymus cinereus</i>	Basin Wild Rye	ELCI	Native ^{a c}
<i>Elymus elmoides</i>	Squirrel-tail	ELEL	Native ^a
<i>Festuca</i> spp.	Fescue (genus only)		Introduced ^a
<i>Festuca occidentalis</i>	Western fescue	FEOC	Native ^{a c}
<i>Hespero-stipa comata</i>	Needle and thread grass	HECO	Native ^{a c}
<i>Hilaria</i> spp.	Curly mesquite (genus only)		Native ^a
<i>Hordeum jubatum</i>	Foxtail barley	HOJU	Native ^{a c}
<i>Koeleria cristata</i>	June Grass	KOCR	Native ^{a c}
<i>Melica bulbosa</i>	Onion grass	MEBU	Native ^{a c}
<i>Nassella viridula</i>	Green needle grass	NAVI	Native ^{a c}
<i>Pascopyron smithii</i>	Western wheatgrass	PASM	Native ^{a c}
<i>Phleum pratense</i>	Timothy	PHPR	Introduced ^{1 2 a}
<i>Poa annua</i>	Annual bluegrass	POAN	Introduced ^a
<i>Poa bulbosa</i>	Bulbus bluegrass	POBU	Introduced ^{1 a}
<i>Poa compressa</i>	Canada bluegrass	POCO	Introduced ^{1 a}
<i>Poa pratensis</i>	Kentucky bluegrass	POPR	Introduced ^{1 a c}
<i>Poa fendleriana</i>	Mutton grass	POFE	Native ^{a c}
<i>Poa secunda</i>	Sandberg blue grass	POSE	Native ^{a c}
<i>Scirpus</i> spp.	Sedge (genus only)		Native ^a
<i>Triticum aestivum</i>	Wheat	TRAE	Introduced ^{1 2 a c}
<i>Vulpia octoflora</i>	Six-weeks grass	VUOC	Native ^a
SHRUBS			
<i>Acer glabrum</i>	Douglas maple	ACGL	Native ^a
<i>Amelanchier alnifolia</i>	Serviceberry, Saskatoon	AMAL	Native ^a
<i>Artemisia cana</i>	Silver sage	ARCA	Native ^{a b}
<i>Artemisia ludoviciana</i>	Mugwort, Medicine sage	ARLU	Native ^{a b}
<i>Artemisia tridentata</i>	Big sagebrush	ARTR	Native ^{a b}
<i>Atriplex canescens</i>	Four-wing salt brush	ATCA	Native ^{a b}
<i>Ceratoides</i> spp.	Winterfat		Introduced ^a

Appendix 1-A. Continued.

Scientific name	Common Name	Code	Native Status
<i>Ericameria nauseosus</i>	Gray Rabbitbrush	ERNA	Native ^a
<i>Chrysothamnus viscidiflorus</i>	Douglas Rabbitbrush	CHVI	Native ^a
<i>Berberis fendleria</i>	Fendler Barberry	BEFE	Native ^a
<i>Gutierrezia sarothrae</i>	Broom snakeweed	GUSA	Native ^{a b}
<i>Hippochaeta</i> spp.	Horsetail (genus only)		No record ^a
<i>Juniperus</i> spp.	Juniper (genus only)		Native ^a
<i>Mahonia Repens</i>	Creeping barberry	MARE	Native ^{a b}
<i>Purshia tridentata</i>	Antelope brush	PUTR	Native ^{a b}
<i>Prunus virginiana</i>	Choke cherry	PRVI	Native ^a
<i>Quercus gambelii</i>	Gambel's Oak	QUGA	Native ^{a b}
<i>Ribies</i> spp.	Gooseberry (genus only)		
<i>Rosa woodsii</i>	Wood's rose	ROWO	Native ^{a b}
<i>Sarcobatus vermiculatus</i>	Greasewood	SAVE	Native ^{a b}
<i>Salix</i> spp.	Willow (genus only)	SALIX	Native ^a
<i>Symphoricarpos oreophilus</i>	Mountain snowberry	SYOR	Native ^a
<i>Tetradymia</i> spp.	Horsebrush (genus only)		Native ^a

Sources: ^a The PLANTS Database (USDA 2003)

^b The Weeds of the West (Whitson et al. 2000)

^c Manual of the grasses of the United States (Hitchcock 1971)

¹ Introduced from Europe

² Introduced from Asia

³ Noxious weed status

Appendix 1-B. Climatic variables from Craig 4 SW weather station in Colorado, 2001-2002 (NOAA 2003). MNTM= mean monthly temperature, TPCP= total monthly precipitation, and difference between 2002 and 2001.

	MNTM (°C)			TPCP (mm)		
	2001	2002	Difference	2001	2002	Difference
January	-10	-8	+2	85	67	-18
February	-5	-8	-3	113	24	-89
March	1	-3	-4	110	119	+19
April	8	8	0	117	120	+3
May	11	11	0	192	13	-179
June	16	19	+3	63	26	-37
July	N/A	22	N/A	91	71	-20
August	20	19	-1	134	196	+62
September	N/A	15	N/A	91	157	+66
October	9	7	-2	134	134	0
November	3	N/A	N/A	129	N/A	N/A
December	-7	N/A	N/A	55	N/A	N/A

CHAPTER 2. AN EVALUATION OF THE TIMING OF GREATER SAGE-GROUSE NEST VEGETATION SAMPLING

INTRODUCTION

Microhabitat sampling for nest use and selection studies of ground nesting sage-steppe birds (Reynolds 1981, With and Webb 1993) and upland game birds (Storaas and Wegge 1987, Kilbride et al. 1992, Rumble and Hodorff 1993, McKee et al. 1998) are made after a female ceases nesting so as not to disrupt incubation. This is also prevalent in habitat studies of greater sage-grouse (Klebenow 1969, Wakkinen 1990, Connelly et al. 1991, Gregg et al. 1994, Musil et al. 1994, Apa 1998, Aldridge 2000). These measurements have limitations; they do not accurately represent vegetation composition and structure at the time of nest site selection as plant growth and/or senescence is ignored (Reese et al. 1987).

Habitat management guidelines of greater sage-grouse currently use post-hatch vegetation characteristics although these may be sampled > 30 days after nest site selection. The impact of this time lag on habitat characteristics is unknown. My objectives were (1) to estimate habitat characteristics at the time of nest initiation at previous years nest sites, (2) to compare those to habitat characteristics measured at the time of hatch, and (3) to predict habitat characteristics incorporating the time lag.

METHODS

To describe the vegetation greater sage-grouse select at the time of nest initiation, vegetation was sampled in 2002 at nest initiation (18 April - 29 April) and at hatch (18 May - 4 June) at 30 nest sites randomly chosen from 40 nests active in 2001. Sixteen of these had

been successful, and 14 had been unsuccessful. All vegetation measurements were the same as in Chapter 1 with the following exception: grass and forb cover were not quantified to nearest taxon.

Vegetation variables were divided into 2 groups, those measured at the nest bowl and those measured in the surrounding area (2.5, 5, and 10 m). Grass height measurements were summarized at 0 and 1 m. Means of cover estimates were obtained by using the mid-point value of each cover class. Variables were assessed for normality and arcsin transformed when necessary. A correlation analysis was performed on the habitat variables to reduce the dimensionality. Visual obstruction measurements read at 5.0 m were correlated to those measured at 2.5 m ($r^2 = 0.57 - 0.90$, $P < 0.001$) and measurements read from 0.5 m were correlated to those read at 1.5 m ($r^2 = 0.78 - 1.00$, $P < 0.001$), thus the latter in both cases was removed from further analysis. The remaining visual obstruction readings were correlated to nest shrub height and also removed from further analysis ($r^2 = 0.36 - 0.74$, $P < 0.004$). Percent shrub cover was correlated to big sagebrush cover and therefore percent shrub cover was removed from further consideration ($r^2 = 0.36$, $P < 0.006$). Understory cover measurements at the nest bowl and averaged over the nest plot were correlated, thus the average values were retained as the values consisted of a greater number of samples (Table 2.1).

I used a randomized complete block design and a multivariate analysis of variance (MANOVA) to assess differences in the remaining 10 microhabitat variables due to timing of vegetation sampling. Paired nest plots were blocked. Evaluation of univariate ANOVA and canonical analysis was used to determine which variables contributed to overall differences. Habitat variables that accounted for differences between initiation and hatch were assessed

for linear correlation based on the date of vegetation sampling (1 – 48 days), corresponding to nest initiation and hatch (SAS Institute 1999).

RESULTS

A difference was detected in vegetation by time of measurement (Wilk's $\lambda = 0.27$; $F = 5.32$; 10,20 df; $P = 0.001$) for the 10 habitat variables. The habitat variables contributing to this difference included grass heights at 0 and 1 m, and average percent grass cover (Table 2.2). Other habitat characteristics, especially those associated with sagebrush heights and coverage, did not differ from initiation to hatch (Table 2.2). Grass height at 0 and 1 m showed a significant linear correlation between initiation and hatch (Table 2.3). The linear regression equations that resulted were grass height in cm at 0 m = $8.93 \text{ cm} + 0.17$ (date of vegetation sampling) and grass height at 1 m = $7.98 \text{ cm} + 0.12$ (date of vegetation sampling) (Figure 2.1). Four outliers were removed from the percent grass cover data set and then analyzed for linear correlation. There was no linear relationship for percent grass cover (Table 2.3).

Using the slope of the regression equations as a constant, 45 days post-initiation as the sampling time, and habitat management guidelines of Connelly et al. (2000), which suggest grass height at hatch to be ≥ 18 cm, grass height at both 0 and 1 m at initiation needs to be ≥ 10.4 cm. However, these management guidelines may have limited applicability in Colorado given that no habitat studies from Colorado are included in deriving this minimum standard. Nest success for the population of greater sage-grouse in the Axial Basin and Danforth Hills was normal to high for both years with 64% and 49% success in 2001 and 2002, respectively. Mean grass heights were 18.9 and 18.3 cm at successful nest in 2001 and

13.4 and 13.8 cm in 2002 (Chapter 1). With these values as guidelines at hatch, grass height at initiation should range from 5.8 - 11.3 cm at the nest plot and 8.4 - 12.9 cm at 1 m.

DISCUSSION

Characteristics of vegetation at the time of initiation may best represent structure females are cueing into for nest site selection. At nest initiation females selected shrubs with a mean height of 82 cm, within a stand of shrubs with average height of 52 cm. Sagebrush canopy cover was 30%. These components corresponded to greater sage-grouse habitat characteristics associated with nest sites at hatch and to those recommended in the literature (Connelly et al. 2000). Grass cover was 4% and heights at initiation were 9-10 cm, which were lower than those reported at time of hatch and as recommended for nesting habitat (Connelly et al. 2000). These were the variables that contributed most to the difference between sampling times.

Grass height at the nest bowl and at 1 m formed predictive linear relations between sampling times from initiation and hatch. Grass height and cover were deemed important for nest site selection and success in the Axial Basin and Danforth Hills (Chapter 1). Linear correlation between variables at initiation and hatch indicated that hens selected characteristics of the herbaceous understory that would serve them best throughout incubation. Additionally, correlations enable managers to predict the change in habitat characteristics over the time frame from initiation to hatch and allow some freedom in the timing of sampling over this period.

The assumptions of this sampling procedure were that there was no variation in grazing by domestic and wild ungulates between years and that the same nest sites in 2001

represented those selected in 2002. The degree of nest fidelity gives the second assumption credibility. The average distance adult females moved between consecutive nests was 0.45 km (Chapter 4). Measurements made at actual nest sites in 2002 ($n = 54$) were compatible to those at nest sites from 2001 at hatch. Grass heights measured in 2001 at the nest bowl and 1 m were similar to those reported at hatch with heights of 12.5 cm, $SE = 0.8$ and 13.6 cm, $SE = 0.8$.

MANAGEMENT IMPLICATIONS

Data collected in this study in 2002 of nests from 2001 provided a more accurate measurement of the nest site characteristics that greater sage-grouse females were selecting without having to disturb incubating females. The only habitat characteristics that differed from the time of initiation to hatch were grass heights and grass cover. Because these variables showed a linear correlation between initiation and hatch, their values can be predicted over the time period between initiation and hatch. Given that nest success for the population is normal to high for the species, I used grass heights measured at hatch in the regression equations to predict a minimum guideline of 6 - 13 cm grass height for nesting measured at clutch initiation. Apart from grass measurements, no other habitat variables differed between sampling times, indicating that current habitat sampling techniques provide an adequate description of nest site characteristics at selection.

Decisions regarding management of nest habitat conditions may be based on range measurements made in the spring. Grazing of cattle begins by 1 May in the Danforth Hills and by early March in the Axial Basin on areas used for nesting by greater sage-grouse. Additionally, controlled burning practices in the Danforth Hills commence in late April and

early May. Therefore, when assessing range conditions at these time periods, minimum structural variables of habitat at the time of nest initiation need to be considered for any ground-nesting species that relies on grass for cover during incubation.

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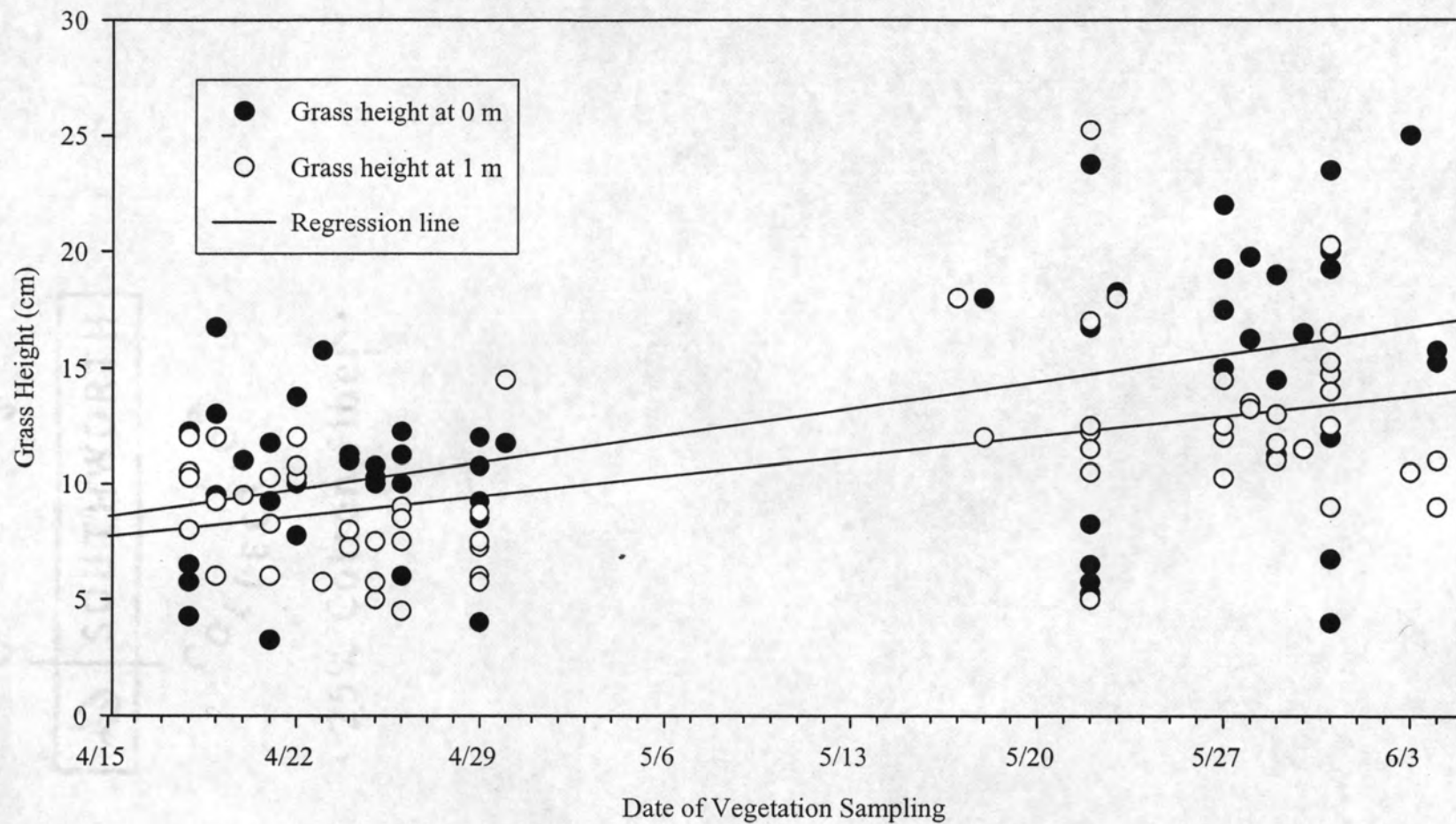


Figure 2.1. Regression of grass heights measured at 0 and 1m at greater sage-grouse nest sites at initiation (4/18-4/29) and nest hatch (5/17-6/4) in Moffat County, Colorado 2002.

Table 2.1. Correlations between understory cover characteristics of greater-sage grouse nest habitat in northwest Colorado. Pearson correlation coefficients and associated P-values are reported.

	Forbs 0 m	Average forbs	Grass 0 m	Average grass	Bare ground 0 m	Average bare ground	Litter 0 m	Average litter
Forbs 0 m P-value	1							
Average forbs P-value	0.604 < 0.001	1						
Grass 0 m P-value	0.078 0.554	-0.108 0.412	1					
Average grass P-value	0.119 0.366	0.081 0.537	0.586 < 0.001	1				
Bare ground 0 m P-value	-0.227 0.081	-0.306 0.018	0.111 0.397	0.204 0.118	1			
Average bare ground P-value	-0.267 0.039	-0.450 < 0.001	0.036 0.784	0.024 0.857	0.396 0.002	1		
Litter 0 m P-value	0.120 0.360	0.270 0.037	-0.475 < 0.001	-0.434 0.001	-0.821 < 0.001	-0.455 < 0.001	1	
Average litter P-value	0.218 0.094	0.376 0.003	-0.204 0.117	-0.186 0.156	-0.350 0.006	-0.928 < 0.001	0.545 < 0.001	1

Table 2.2. Mean and standard error (SE) for habitat variables included in MANOVA at initiation (4/18-4/29) and hatch (5/17-6/4) for 30 greater sage-grouse nests from 2001 measured in 2002 in the Axial Basin and Danforth Hills, Colorado.

Variable	Initiation	SE	Hatch	SE
Cover board	15.4	0.05	13.6	1.4
Percent sagebrush cover ^a	29.9	2.6	29.9	2.8
Nest shrub height (cm)	81.9	3.5	82.8	3.7
Average shrub height (cm)	51.9	3.1	52.7	3.3
Grass height 0 m (cm) ^b	10.0	0.6	15.6	1.1
Grass height 1 m (cm) ^c	8.5	0.4	13.3	0.7
Average forb cover ^a	3.8	0.7	5.1	0.9
Average grass cover ^{a,d}	3.5	0.4	5.5	0.8
Average bare ground ^a	15.9	2.5	14.0	2.3
Average litter cover ^a	80.5	2.4	82.1	2.5

^a Arcsin transformed for MANOVA, untransformed mean and SE are reported

^b $F = 43.36$, $P < 0.001$

^c $F = 32.99$, $P < 0.001$

^d $F = 5.86$, $P = 0.022$

Table 2.3. Coefficient of determination (r^2) for habitat characteristics measured over a sampling gradient of initiation to hatch for 30 greater sage-grouse nest sites sampled in 2002 in northwest Colorado.

Variable	F-value	P-value	r^2
Grass height at 0 m	22.70	< 0.001	0.281
Grass height at 1 m	24.32	< 0.001	0.295
Average grass cover	2.93	0.093	0.052

CHAPTER 3. NOCTURNAL AND DIURNAL HABITAT SELECTION OF GREATER SAGE-GROUSE DURING BROOD-REARING IN NORTHWEST COLORADO

INTRODUCTION

Brood-rearing habitat

An important feature of brood-rearing habitat of greater sage-grouse is cover adjacent to food in the form of insects and forbs (Klebenow 1972, Sveum et al. 1998). Insects dominate the diet of chicks in their first 2 weeks (Peterson 1970), with the main insects consumed being grasshoppers (Orthoptera), beetles (Coleoptera), and ants (Hymenoptera) (Knowlton and Thornley 1942, Klebenow and Gray 1968, Drut et al. 1994).

As chicks develop, their diet shifts to forbs and succulent shrubs (Patterson 1952, Klebenow and Gray 1968, Klebenow 1969, Peterson 1970, Klebenow 1972). This may also coincide with habitat desiccation (Fischer et al. 1996a). Distinct summer habitat preferences are exhibited by some populations (Schoenberg 1982, Connelly et al. 2000).

Early brood-rearing sites tend to be in big sagebrush habitat close to nest areas. Wakkinen (1990) noted a shift in late brood-rearing habitat to more mesic sites as forbs began to desiccate. Fischer et al. (1996a) related this movement to vegetal moisture content of $\leq 60\%$ water. Summer migration has been documented as either upwards to upland meadows (Savage 1969), or downward in elevation to riparian areas following a gradient of forbs (Klebenow 1969).

Night-Roost Habitat

Despite extensive research into the habitat requirements of greater sage-grouse, summer night-roosting habitat has received no attention. Previous research has included winter night-roost sites (Beck 1977) and male night-roost preferences during the breeding season (Patterson 1952, Wallestad 1971, Klebenow 1972, Emmons and Braun 1979). Authors have speculated that during the spring and summer greater sage-grouse select open cover types in which to breed and feed (Klebenow 1972, Blus et al. 1989, Nelle et al. 2000) and dense habitat in order to roost.

By late summer, grassland grouse populations abandon the tactic of inconspicuousness and join gang broods (Bergerud 1988). Patterson (1952) indicated that a single greater sage-grouse roost area in the fall and winter might encompass dozens of acres and involve hundreds of birds. There is no indication in the literature as to what role, if any, social structure plays on nocturnal habitat use.

A more complete understanding of greater sage-grouse habitat use is imperative for reversing population declines. By considering temporal variation in habitat use patterns habitat management guidelines can promote and protect critical habitat needs. The objectives of this study were to (1) model brood productivity and brood and night-roost habitat selection and (2) compare nocturnal and diurnal habitat use during the brood-rearing period.

METHODS

Females with broods were located, at randomly selected time periods from dawn to dusk, via radio-telemetry 1-2 times per week. Additionally, individual females with and

without broods were located at ≥ 1 hour before sunrise and ≥ 1 hour after sunset from 4-10 weeks post-hatch. A count of individuals at each night roost location was made using binoculars and a spotlight (Wakkinen et al. 1992). At each diurnal location cover type, date, time, UTM coordinates, slope, aspect, distance to nearest visual obstruction and distance to nearest 2-track were recorded. An estimate of brood size was made 6 weeks post-hatch by flushing radio-marked females that had been successful at hatching a nest. Productivity was calculated by dividing the total number of chicks flushed at 6 weeks by the number of females alive and radio-marked at the start of the breeding season. A Van der Waerden test was used to assess variability in productivity among years, as the data did not fit a normal distribution (Conover 1999)

Individuals located nocturnally were restricted to those within a 15-minute walk from the nearest road, thus distance to road was not included in our analysis as our sample design biased this variable. Each week, for 10 weeks post-hatch, 25% of radio-marked hens with broods were randomly chosen for diurnal vegetation sampling. I estimated the center of brood activity by locating the hen visually. Sites were marked and sampled within 3 days after the brood had left the vicinity. All vegetation measurements at brood use locations were the same as at nest sites (Chapter 1) with the following exceptions: 1) grass and forb height were quantified by measuring the nearest individual within 1 m of plot center, and within 1 m of each transect at 2.5, 5.0, 7.5 and 10 m, 2) a single 40 x 50 cm microplot was placed at the point where the transects met and at 2.5, 5.0, 7.5, and 10 m along each transect, and 3) no cover board was used at the transect intersection.

Random locations were selected from northing and easting UTM coordinates falling within the home range of the population and were measured within 1 week of vegetation

sampling at the brood use area using identical techniques. Random sites occurring in shrub-steppe, mountain shrub, CRP, riparian, wet meadow, and agricultural cover types were accepted as potential brood-rearing locations.

There were 173 plant species identified at brood, night roost and random sites over the 2 years of study (Appendix 1-A). Thus, analyzing cover by individual plant species was not feasible compared to the number of plots sampled. Instead, I summarized individual plant species by their frequency of occurrence within each plot and ranked them by their abundance within brood, night-roost and random locations.

Flock size

A correlation matrix of structural habitat characteristics was examined to control for multicollinearity. Visual obstruction readings read at a height of 1.5 m were correlated ($r^2 > 0.80$, $P < 0.001$) to those read at 0.5 m and therefore removed from flock size analysis. Additionally 0-0.5 m and 0.5-1.0 m demarcations of visual obstruction read from a height of 0.5 m and a distance of 5 m were correlated thus the visual obstruction reading from 0.5-1.0 m was also removed from further analysis. Forward stepwise multiple regression analysis was used to determine the model that would best predict flock size with the fewest structural habitat characteristics (Ott and Longnecker 2001). A significance level of $P \leq 0.10$ was used to determine which variables entered and remained in the model. Variables considered were shrub, grass and forb height, visual obstruction readings from 0-0.5 m and read from 2.5, 5 and 10 m., and visual obstruction readings from 0.5-1.0 m and read from 5 and 10 m.

Vegetation Sampling

I partitioned the variables of slope, aspect and distance to nearest structure into the same categories as described in Chapter I. Elevation received an additional categorization;

low ($< 2,020$ m), medium (2,021-2,140 m), medium- high (2,141-2,160 m) and high ($> 2,160$ m). Prior to examination, variables were assessed for correlation strength (Ott and Longnecker 2001). I used chi-squared tests to determine whether there were macrohabitat differences between years at brood sites. Chi-squared tests were also conducted between random and brood-use sites, random and night roost locations, and diurnal and nocturnal sites.

The mean of each vegetation variable over the plot was used in all calculations. Means of cover estimates were obtained by using the mid-point value of each cover class. Variables were assessed for normality and arcsin transformed when necessary. I used a multivariate analysis of variance (MANOVA) to assess whether microhabitat variables differed at random locations between years ($P \leq 0.05$) (Johnson and Wichern 2002). Those that differed were assessed for correlation strength. A principal component analysis was conducted on the characteristics of the random locations that did not differ between years (Johnson and Wichern 2002). Brood and night-roost sites were scored with the principal components generated from the random plots. Forward step-wise logistic regressions included the principle components, habitat variables that differed between years and the class variable year. These were used to test the importance of the habitat variables in predicting 1 of 2 binary variables; brood site or random, night-roost or random and diurnal or nocturnal use site. A significance level of $P \leq 0.10$ was used to determine which variables entered the model. This analysis was performed in SAS 8.2 (SAS Institute 1999).

Early/Late Brood-rearing

Brood habitat has typically been separated into that used for early and late brood-rearing (Drut et al. 1994). I further defined this split as the date when 90% of radio-marked

hens changed cover type to either mountain shrub or riparian/wet-meadow communities and/or had moved up or down in elevation. During 2001, early brood-rearing appeared to end 7 July and late brood-rearing terminated at the end of data collection in August. In 2002, early brood-rearing ended by 14 July and late brood-rearing continued through August when field work was completed. I used a correlation analysis to reduce the dimensionality of the data set and then a MANOVA to assess whether habitat differences occurred between early and late brood-rearing time-periods. Analysis of canonical variables and univariate ANOVA was used to determine which variables contributed to the differences.

RESULTS

Brood Size

Brood sizes at 6 weeks ranged from 0 to 8 chicks. In 2001 the mean number of chicks per female that successfully hatched a nest was 3.5, $SE = 0.4$, $n = 26$, which did not differ ($t = 1.9$, $P = 0.064$) from the mean number of chicks per female, 2.4, $SE = 0.4$, $n = 29$ in 2002. Pooling the data over both years resulted in an estimate of 3.0 chicks/successful female at 6 weeks of age. Mean productivity in 2001 (1.5 chicks/female alive at the beginning of nesting, $SE = 0.3$, $n = 60$) did not differ ($Z = 8.05$, $P = 0.214$) from 2002 (1.0 chick/female, $SE = 0.2$, $n = 73$).

Flock Size

Flock sizes at nocturnal use sites ranged from 1 to 30 individuals, with mean flock size at 6.0 individuals ($SE = 0.82$, $n = 58$). Forward stepwise multiple regression analysis produced a model with visual obstruction from 0-0.5 m, read from a height of 0.5 m and a distance of 5 m and visual obstruction reading from 0.5-1.0 m, read from a height of 0.5 m

and a distance of 10 m, as the only significant predictors of flock size at night-roosts (Table 3.1). Flock size declined with increasing visual obstruction when read close to the flock (5 m) at ground level (0-0.5 m) and increased with increasing visual obstruction from the furthest reading distance (10 m) and between the heights of 0.5-1.0 m.

Vegetation Sampling

Macrohabitat.

Proportional use of aspect and elevation differed between years at brood-use sites ($\chi^2 = 15.43, 4 \text{ df}, P = 0.004, \chi^2 = 12.90, 3 \text{ df}, P = 0.005$), respectively. The difference in aspect was due to a higher proportion of locations falling in the 0° slope category in 2001 (25%) than 2002 (7%). For elevation the difference resulted from higher proportional use of the low elevation category (50 vs. 35%) in 2001 than in 2002. The means, however, between years for these variables fell within the same category (aspect: $136\text{--}187^\circ$, elevation: 2021-2140 m). These characteristics were not pooled for further analysis. In 2001, greater sage-grouse broods were found at a greater proportion within the high elevation category (17 vs. 2%) and less in the medium-high category (9 vs. 26%) ($\chi^2 = 14.74, 3 \text{ df}, P = 0.002$) compared to random (Table 3.2). Additionally, relative brood use tended to be less (10 vs. 41%) within aspects ranging from $136\text{--}314^\circ$ ($\chi^2 = 20.13, 4 \text{ df}, P = 0.001$) than random. In 2002, mean elevation at greater sage-grouse brood and random sites was 2,117, $SE = 23, n = 92$ and 1,978, $SE = 17, n = 93$, respectively and proportional use did not differ ($\chi^2 = 6.58, 3 \text{ df}, P = 0.373$). Relative use of aspect at brood sites did not differ from random ($\chi^2 = 4.25, 4 \text{ df}, P = 0.097$). Combining years, no relationship was detected between proportional brood and random site use with respect to distance to nearest visible structure ($\chi^2 = 0.30, 2 \text{ df}, P =$

0.862), distance to nearest two-track ($\chi^2 = 4.38$, 2 *df*, $P = 0.112$) or mean slope ($\chi^2 = 5.13$, 2 *df*, $P = 0.077$) (Table 3.2).

No differences were detected among relative use of physical macrohabitat characteristics at night-roost sites between years and so the data were pooled ($P > 0.341$). Additionally, no relationship was found with regards to relative use of slope ($\chi^2 = 3.39$, 2 *df*, $P = 0.183$) and distance to structure ($\chi^2 = 0.14$, 2 *df*, $P = 0.930$) for night-roost and random locations (Table 3.2). A relationship was found with regards to relative use of aspect ($\chi^2 = 14.27$, 4 *df*, $P = 0.007$), and elevation ($\chi^2 = 29.21$, 3 *df*, $P < 0.005$) for greater sage-grouse night-roost locations. Greater sage-grouse night-roost locations were found at a greater proportion within the northerly aspect category (43 vs. 19%) and within the medium-high (38 vs. 16%) elevation category than random sites.

Comparison of physical macrohabitat characteristics among diurnal and nocturnal brood sites revealed no differences of relative use of slope ($\chi^2 = 0.12$, 2 *df*, $P = 0.941$) or distance to nearest visible structure ($\chi^2 = 0.01$, 2 *df*, $P = 0.994$) (Table 3.2). In 2001, no difference was detected with proportional use of aspect ($\chi^2 = 6.20$, 4 *df*, $P = 0.185$), however, night-roost locations tended to fall within the medium-high elevation category to a greater extent (39 vs. 9%) than diurnal locations ($\chi^2 = 11.76$, 3 *df*, $P = 0.008$). No relationships between diurnal and nocturnal locations were detected for relative use of aspect or elevation in 2002 ($\chi^2 = 5.60$, 4 *df*, $P = 0.231$; $\chi^2 = 0.07$, 3 *df*, $P = 0.996$) (Table 3.2).

Microhabitat.

Microhabitat characteristics differed at random sites ($F = 5.65$, $P < 0.005$) between years. Vegetation characteristics that varied between years at random locations were species richness, percent cover of forbs, exotics and bare ground, visual obstruction from 0-0.5 m

measured from a reading location of 5 m and a reading height of 0.5 m, visual obstruction from 0-0.5 m measured from a reading location of 10 m and a reading height of 0.5 m, and visual obstruction from 0.5- 1.0 m measured from a reading location of 2.5 m and a reading height of 0.5 m (Table 3.3). Visual obstruction from 0-0.5 m read from reading height of 0.5 m at 10 m and visual obstruction 0.5-1.0 m read from a reading height of 0.5 m and a distance of 2.5 m were correlated ($r^2 = 0.83$, $P < 0.005$, $n = 94$), thus the latter reading was removed from further analysis. Additionally, species richness and percent forb cover were correlated ($r^2 = 0.68$, $P < 0.001$, $n = 94$). Species richness was removed from further analysis. I conducted a PCA on the 15 habitat characteristics of 94 random sites, minus the 5 variables; percent cover of forbs, exotics and bare ground, and visual obstruction from 0-0.5 m, read from a height of 0.5 m and from the distances 5 and 10 m which contributed to the significant difference between years. This produced a description of the structural habitat gradients within the study area. The PCA defined 4 principal components, accounting for 78% of the overall variance. Each of the principal components considered had an Eigenvalue >1 (Table 3.4).

The 4 principal components each described an ecologically interpretable gradient. The first component, described a complex gradient of structure with the scale ranging from herbaceous cover to tall shrubs, high proportion of shrub cover including sagebrush and high visual obstruction from 0-1 m. This addressed the overall physiognomy of the sage-steppe community. The second and third components related to the shrub-steppe under-story community. The second component varied along a gradient of herbaceous cover from a high percent grass cover at the positive end of the gradient, with grass and forb height and percent litter at the negative end of the gradient. The third principal component was defined by grass

height on the positive end of the gradient and visual obstruction at ground level (< 50 cm) on the negative end. The fourth component defined community complexity with high shrub cover, sagebrush cover and grass height on the positive end of the gradient and visual obscurity from 0-1 m read from 2.5 m at a height of 1.5 m falling on the negative end of the gradient (Table 3.4).

Ten variables entered all 3 forward step-wise logistic regressions. These included year, principle components 1-4, and the variables that differed between years; percent forb, exotic and bare ground cover, and 2 visual obstruction readings, VISOBa12 and VISOBa13. Logistic regression found percent forb cover, percent bare ground, and visual obstruction readings from 0-0.5 m, a reading height of 0.5 m and from 5 and 10 m, to be significant predictors of brood occurrence (Table 3.5). The logistic regression equation that resulted was: $\text{Logit}(Y) = -0.9 + 31.7 (\text{PCTFORB}) - 3.7 (\text{BRGROUND}) - 0.8 (\text{VISOBa12}) - 0.7 (\text{VISOBa13}) + e$ (Table 3.5). The logit transformation allows one to describe the relationship between the binary response variable and multiple explanatory variables and the e represents error in the model (Ott and Longnecker 2001). Percent forb cover and visual obstruction readings from 0-0.5 m, a reading height of 0.5 m and from 5 and 10 m were all greater at brood sites than at random (Table 3.6). Mean bare ground cover was the only variable less at brood sites than at random sites.

Logistic regression was also used to predict night-roost selection. The habitat variables that entered the model as significant predictors of night-roost locations were percent forb and bare ground cover, VISOBa12 and VISOBa13 (Table 3.5). The logistic regression equation that resulted was: $\text{Logit}(Y) = 0.7 + 14.5 (\text{PCTFORB}) - 2.9 (\text{BRGROUND}) - 0.9 (\text{VISOBa12}) - 0.4 (\text{VISOBa13}) + e$ (Table 3.5). Percent forb cover was

greater at night-roost locations than at random locations, while bare ground, VISOBa12 and VISOBa13 values were all less at night-roost locations than at random locations (Table 3.6).

Finally, logistic regression was used to predict nocturnal versus diurnal occurrence. The habitat variables that entered the model as significant predictors of night-roost locations were PC 1, percent cover of exotics, and VISOBa12 (Table 3.5). The logistic regression equation that resulted was: $\text{Logit}(Y) = 1.5 - 0.7(\text{PC } 1) - 2.2(\text{EXOTICS}) - 1.5(\text{VISOBa12}) + e$ (Table 3.5). PC 1 involved percent shrub cover, sagebrush cover, shrub height, and all the visual obstruction readings (Table 3.4). All the values within PC 1, percent cover of exotics and visual obstruction 0-0.5m read from a height of 0.5 m and from a distance of 5 m were greater at diurnal sites than at nocturnal sites (Table 3.6).

Individual Plant Frequency

Because the MANOVA indicated that there were vegetation differences between years, particularly among forb cover (Table 3.3), I analyzed plant frequency separately for 2001 and 2002. In 2001, the most abundant shrub species at brood sites was sagebrush (Figure 3.1). Forbs found in > 60% of plots included pale madwort, maiden blue-eyed Mary, longleaf phlox, onion (*Allium* spp.), clover and common salsify (*Tragapogon dubius*) (Figure 3.1). Grasses that occurred in > 60 % of brood sites included western wheatgrass, cheat grass and Sandberg bluegrass (*Poa secunda*). The same species were abundant at random sites with some exceptions. Dead sagebrush and copper mallow occurred at > 60% of random locations and common salsify only occurred at 30% of random locations (Figure 3.1).

The most abundant shrub species at night-roost sites was dead sagebrush (Figure 3.2). Nocturnal sites had less sagebrush occurring than random. Forbs found in > 60% of night-roost locations include pale madwort, buttercup (*Ranunculus muricatus*), longleaf phlox,

maiden blue-eyed Mary and common salsify. Grasses at > 60% of night-roost locations included Sandberg bluegrass, western wheatgrass and cheat grass. Common salsify occurred at 64% of night-roost plots and only 31% of random locations (Figure 3.2).

In 2002, the most abundant shrub species at brood sites were sagebrush and dead sagebrush (Figure 3.3). Forbs found in > 60% of plots included only longleaf phlox and maiden blue eyed Mary. Abundant grasses included western wheatgrass and Sandberg bluegrass. In 2002, the majority of the most abundant species of forbs (maiden blue-eyed Mary, common salsify, lupine) occurred more frequently at brood sites than random indicating that hens were associating with these forbs for brood-rearing (Figure 3.3).

The most abundant shrub species at night-roost locations in 2002 was dead sagebrush (Figure 3.4). Forbs and grasses at > 60% of night-roost locations included pale madwort, longleaf phlox, western wheatgrass, cheat grass, and *Poa* spp. Pale madwort, sagebrush and globe mallow all occurred more frequently at random locations than night-roost locations in 2002.

Early/Late Brood-rearing

Early brood-rearing locations were primarily in shrub-steppe (58%). Broods were also found in mountain shrub (19%), burnt shrub-steppe communities (13%), CRP (8%) and riparian/ wet meadows (2%). Late brood-rearing sites were found with increased frequency in mountain shrub (37%) and riparian (11%) and reduced frequency in shrub-steppe (37%), burnt shrub-steppe (10%) and CRP (4%). The MANOVA on random plots indicated a difference among habitat variables between years (Table 3.3), thus timing was assessed separately for 2001 and 2002. Analysis of early and late brood-rearing indicated a difference in 2001 (Wilk's $\lambda = 0.47$; $F = 1.9$; 22,36 df; $P = 0.047$) but not in 2002 (Wilk's $\lambda = 0.29$; $F =$

1.12; 22,10 df; $P = 0.445$). The habitat variables contributing to the differences in early and late brood-rearing in 2001 were visual obstruction reading 0.5-1.0 m and a reading height of 1.5 m and from a distance of 10 m, visual obstruction readings 0-0.5 m and read from a reading height of 1.5 m and a distance of 2.5 and 10 m and percent forb cover and percent sagebrush cover (Table 3.7). Forb cover was greater at late-brood rearing sites while sagebrush cover was reduced. Visual obstruction decreased at the ground level but increased from 0.5- 1.0 m (Table 3.7).

DISCUSSION

Brood Size

The use of flush counts as an estimate of brood size is inherently biased. Estimates can be either too low if chicks fail to flush or too high if females adopt chicks or broods congregate (N. Burkepile, personal communication). I used flush counts at 6 weeks of age to reduce these biases. An assumption of flush counts is that these biases are consistent between years and locations; therefore brood counts can be used as an index of trend. Mean brood size at 6 weeks post-hatch in 2001 (3.5) was greater than that in 2002 (2.4) by > 1 chick. Although not significant, this difference may have resulted from less forage and cover due to the hot, dry conditions in 2002. Estimates of brood productivity from harvest data collection on Cold Spring Mountain, Blue Mountain and eastern Moffat County, Colorado from 1976-1998 ranged from 0.2-5.0 chicks/female with a mean of 2.0 chicks/female (CDOW, unpublished data). Mean productivity from 1976-1998 from North Park, Jackson County was 1.5 chicks/female (CDOW, unpublished data). Productivity of 2.25 chicks/female has been considered necessary to maintain a stable or increasing population

(Connelly et al. 2000). However, data in North Park shows chicks/female < 2 from 1985-2000, a period when the population size increased. Estimates of brood productivity in the Axial Basin and Danforth Hills (1.5 and 1.0 chicks/female in 2001 and 2002) were below the management recommendations and the means reported in other populations in Colorado. Population trends in Moffat County indicated a decline in population abundance although nest success and adult survival do not appear to be limiting factors (Chapter I, Chapter IV). Although brood counts are likely biased low, these productivity estimates warrant further research into chick survival which may be limiting the population.

Macrohabitat

Differences in relative use of macrohabitat characteristics between brood and random sites were found in 2001 as a greater proportion of brood use-sites were in the high elevation category ($> 2,160$ m) and less in the medium-high elevation category (2,141- 2,160 m) compared to random. Additionally, relative brood use was lower in the southerly and westerly aspect categories ($136-314^\circ$) than random. These results may have been from a greater number of females raising broods in the Danforth Hills than at random from within the study site. Typically females with broods move upwards in elevation during the late brood-rearing period, following a gradient of forbs (Fischer et al. 1996a). The Danforth Hills, which provided much of the late brood-rearing habitat, are higher in elevation, steeper in gradient, and are primarily northerly in aspect.

The differences occurring among relative use of physical macrohabitat characteristics between night-roost locations and random sites were with respect to aspect and elevation. The reasons for these differences are likely due to our sampling protocol. Locations were only obtained for grouse that were within a 15 minute walk from the nearest two-track.

Many night-roost locations were restricted to the Danforth Hills (37 vs. 21), which had a higher concentration of roads than that of the Axial Basin. Similarly, data for 2001 revealed that nocturnal locations were at higher elevations in a greater proportion than at diurnal locations. Again, I sampled more night-roost (71%) than brood locations (44%) in the Danforth Hills than in the Axial Basin.

Macrohabitat characteristics were basically used in proportion to random. These results may be due to the fact there was little habitat diversity within the physiographic characteristics at my study sites (Porter and Church 1987, Åberg et al. 2000). Despite the apparent homogeneity of the shrub-steppe community, selection was apparent at the microhabitat scale.

Brood-site selection

Habitat variables that were significant predictors of brood site selection were percent cover of forbs, bare ground, and visual obstruction readings from 0-0.5 m. Greater sage-grouse females selected brood-rearing sites with higher forb cover and less bare ground than at random locations. Indeed, there was twice as much forb cover at brood sites (8%), than at random locations (4%). These cover values are based on the means of midpoints and would all fit into the vegetation cover category of 3-9%. Previous studies reported broods selecting areas related to forb cover (Klebenow 1969, Peterson 1970, Autenreith 1981, Drut et al. 1994, Apa 1998, Sveum et al. 1998). My forb cover values were similar to those reported by Dunn and Braun (1986) in Moffat County (5%), Schoenberg (1982) in North Park Colorado (7%) and Apa (1998) in southeastern Idaho (8%). However, other researchers have reported forb cover values at brood sites as greater than these; 17-27% in central Montana (Wallestad 1971) and 10-25% in Oregon and Washington (Drut et al. 1994, Sveum et al. 1998). Forbs

have greater protein potential than other vegetation types (Peterson 1970) and have been associated with invertebrate biomass in sagebrush cover-types (Jamieson et al. 2002).

Johnson and Boyce (1990) showed experimentally that insufficient insects in the diet of chicks resulted in deaths from malnutrition. Similarly, arthropod abundance within the first 10 days of hatching was directly correlated to survival in partridge chicks (*Alectoris rufa* and *Perdix perdix*) (Green 1984). Greater sage-grouse females are likely selecting sites with greater forb cover in order to provide forage in the form of invertebrates and forbs for their broods. Less bare ground at brood sites than at random sites supports this hypothesis.

Preference for individual plant species was more apparent in 2002, possibly due to drought conditions. Forbs and grasses such as maiden blue-eyed Mary, onion, Sandberg bluegrass, common salsify and clover were common in 2001 but scarce in 2002. The selection for areas of greater forb cover was apparent in 2002 as forb species occurred less frequently at random locations than brood-use sites. Common salsify has been reported as a major forage item for greater-sage grouse and occurred with twice the frequency at use locations than at random. Globe mallow and cheat grass were not as prevalent at brood sites than at random sites, as these plants indicate dry, open habitat types (Kershaw et al. 1998). The major forbs known to be important in greater sage-grouse diets include common dandelion (*Taraxacum officinale*), milkvetch (*Astragalus* spp.), sego lily (*Calochortus* spp.), yarrow (*Achillea millefolium*), prickly lettuce (*Lactuca* spp.), lupine, and hawksbeard (*Crepis* spp.) (Fischer et al. 1996b). Of these, common dandelion, lupine, and yarrow occurred more frequently at brood sites than random, suggesting selection for these forage items.

Early/Late Brood-rearing

In 2001 there were differences in early and late brood-rearing with respect to forb cover, sagebrush cover and visual obstruction readings. Females with broods moved to areas with greater forb cover, less visual obstruction at ground level and greater visual obstruction from 0.5-1.0 m. Increased use of the mountain shrub communities in the late brood-rearing period supports this trend of greater forb cover, less ground level visual obstruction but greater vertical visual obstruction. Mean sagebrush canopy cover at brood sites in the study area was 11%, however it decreased from 13% to 8% as hens moved into mountain shrub communities from early to late brood-rearing. In 2002, no differences were observed between early and late-brood rearing. Sample size for the late brood-rearing period was small, thus results should be viewed cautiously. Due to the drought in 2002, there was not an abrupt change in habitat, but rather a continuous selection for areas with greater moisture and thus more forbs and insects.

Night-roost Habitat Selection

Nocturnal locations ($n = 58$) were in burnt shrub-steppe (52%), shrub-steppe (38%), grassy meadows (7%), CRP (2%) and riparian (2%) cover types. My results indicated that greater sage-grouse females choose night-roost sites with less bare ground and visual obstruction, but greater forb cover than that at random sites. Night-roost habitat information for greater sage-grouse is limited primarily to males during the breeding season. Patterson (1952), Wallestad (1971) and Klebenow (1972) noted that roosts near leks chosen by males and non-nesting females contained the heaviest and densest sagebrush. In contrast, Emmons and Braun (1979) found 90% of male sage-grouse chose nocturnal roosts directly on leks in order to maintain their strutting positions. Canopy cover of these roost sites was only 8.7%

and shrub height averaged 18.7 cm. Shrub canopy cover of 9.5% and mean shrub height of 30.5 cm characterized nocturnal sites chosen by females in the Axial Basin and Danforth Hills. Night-roost habitat characteristics existing for other ground-roosting upland game birds support our results. Northern bobwhite quail (*Colinus virginianus*) preferred open canopy, short herbaceous cover (30-90 cm) and limited litter at night-roost sites (Klimstra and Ziccardi 1963, Barnes et al. 1995), while ring-necked pheasants (*Phasianus colchicus*) chose herbaceous cover over sagebrush for winter night-roosts in southern Idaho (Leptich 1992). Scaled quail (*Callipepla squamata*) selected nocturnal areas with low shrub cover (Stormer 1984) and Montezuma quail (*Cyrtonyx montezumae*) selected grassy slopes within an oak savanna habitat (Stromberg 1990).

Wind significantly affects greater sage-grouse metabolism (Sherfy and Perkins 1995) and, in instances where greater sage-grouse roosted in shrub-steppe cover type, the birds seemed to be there as a result of inclement weather. The shrub-steppe microclimate effectively reduces exposure to wind (Sherfy and Perkins 1995). Bobwhite quail also exhibited shifts in night-roost locations to more protective cover associated with wind (Klimstra and Ziccardi 1963).

Two potential explanations exist for the selection of open cover types for night-roosting during the summer. First, night-roost locations have higher forb cover than random locations and perhaps provide forage opportunities in the crepuscular periods. Savage (1969) found broods fed in early mornings and evenings and loafed in sagebrush midday. Dunn and Braun (1986) found that greater sage-grouse broods fed in open cover types in the morning while Sveum et al. (1998) reported 52% of afternoon locations occurred in grassland cover types. Potentially, females roost in an open cover type in order to exploit the area for

foraging in the crepuscular periods, particularly for broods, which exhibit high energetic demands. Secondly, open cover types may be chosen in order to provide grouse with greater escape potential from predators. Their large body size and short legs make it laborious for them to initiate flight (Patterson 1952). Open habitat not only provides greater potential of detecting approaching mammalian predators but also minimal interference when flushed, thus facilitating rapid escape.

Selection for individual forb species at nocturnal use sites may support the hypothesis that open habitat types are selected for feeding. Common salsify has been reported as a major forage item for greater sage-grouse, and occurred with twice the frequency at use locations than at random. Other major forb species, common dandelion, lupine, and yarrow, occurred more frequently at brood sites than random, suggesting selection for these forage items. The species that was most strongly avoided at night-roost locations was big sagebrush, confirming the hypothesis that greater sage-grouse select open habitat types in order to night-roost during the summer.

Flock Size

The formation of flocks is thought to decrease vulnerability, as there are effectively more individuals to detect predators (Reynolds et al. 1988). Individual greater sage-grouse roosting sites are in close proximity to other birds during the breeding season, fall and winter (Patterson 1952). With a mean of 6 individuals per roost sites my results indicate that communal roosting is also practiced during brood-rearing. This could be when and where brood-mixing occurs. Bergerud (1988) suggested communal roosting occurred in late summer for open-dwelling grouse populations. Patterson (1952) speculated this behavior served as a means of avoiding night attack by natural enemies. Potential night predators

included red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), and great horned owls (*Bubo virginianus*).

Of the variables examined, visual obstruction readings were the factors related to flock size; flock size decreased with increased visual obstruction read close to the flock (2.5 m) at ground level (0-0.5 m) and increased with increased visual obstruction from the furthest reading distance (10 m) and between the heights of 0.5-1.0 m. This indicates greater sage-grouse required either ground level cover at night-roost locations or larger flock size for increased vigilance from mammalian predators. Increased cover above ground level decreases flock size perhaps indicating that nocturnal avian predation is not a factor influencing vigilance. Examination of carcasses retrieved within 5 days (mean = 2.4 days, $n = 17$) of death supports this hypothesis because I attributed 73% ($n = 8$) of known mortalities to mammalian predation and 9 % ($n = 1$) of known mortalities to great horned owls (Chapter IV).

Nocturnal Versus Diurnal Habitat Selection

Research on greater sage-grouse nocturnal roost sites in the winter has produced contradictory results. Beck (1977) followed greater sage-grouse to their nocturnal sites on their winter range in Jackson County, Colorado, and found that nocturnal roosting sites had the same vegetal and physical characteristics as feeding sites. However, Dalke et al. (1963) suggested that daytime loafing and feeding cover types were not the same as roosting sites.

Authors have speculated that during the spring and summer greater sage-grouse select open cover types in which to breed and feed and seek out denser habitat in order to roost (Klebenow 1972, Blus et al. 1989, Nelle et al. 2000). My results indicated that night-roost locations were different from daily-use sites during brood-rearing in terms of shrub cover.

However, contradicting previous speculation, females with broods selected less dense habitat in which to night roost. Mean shrub cover and shrub height at night roost locations was less dense (9% vs. 22%) and shorter (31 vs. 58 cm) than at diurnal brood-sites. Sagebrush cover was also less dense (4% vs. 11%) at nocturnal use sites. Additionally, the visual obstruction readings were all greater at diurnal sites (Table 3.4). Patterson (1952) noted a tendency for sage-grouse to select taller sagebrush in draws and gullies in order to roost in the daytime, in contrast to the smaller and more open sagebrush areas selected at night.

MANAGEMENT IMPLICATIONS

Habitat management guidelines recommend > 10% forb cover for brood-rearing (Connelly et al. 2000). Forb cover of 8%, which falls into the cover category of 3-9%, was selected by females for brood-rearing in the Axial Basin and Danforth Hills and falls short of this recommendation. However, the influence of this on survival of chicks is unknown. Changes in availability of forbs greatly influence grouse distribution and habitat selection. In Oregon, greater sage-grouse reportedly had larger home range sizes in areas having low forb abundance (Drut et al. 1994). The affinity of greater sage-grouse broods for areas of greater forb cover offers management opportunities. Practices such as seeding with exotic grasses, herbicide treatments and widespread burning should be avoided. Greater sage-grouse broods are more reliant on invertebrate foods than adult birds (Wallestad et al. 1975). Management practices that improve habitat for broods may be extremely beneficial as low brood productivity may be a factor limiting this greater sage-grouse population.

Despite extensive research into the habitat requirements of greater sage-grouse, night-roosting habitat received little attention. Current habitat management guidelines apply only

to diurnal habitat needs and should be viewed cautiously (Beyer and Haufler 1994). I recommend that managers consider night-roosting habitat characteristics of broods a critical component of greater sage-grouse habitat requirements.

Present literature on diurnal habitat use by broods does not recognize the importance of openings in the shrub-steppe community specifically for night roosting. Habitat guidelines recommend sagebrush cover ranging between 10-25% (Connelly et al. 2000). Fischer et al. (1996b) concluded that the short-term effect of fire does not serve to enhance brood habitat in southeastern Idaho. However, their results are based upon sampling procedures that occurred diurnally. Therefore, they may have missed greater sage-grouse nocturnal use of burnt areas. My results indicate greater sage-grouse seek out openings with $< 5\%$ sagebrush cover and $< 10\%$ shrub cover such as recently burnt shrub-steppe communities in order to roost. Therefore, I would agree with Klebenow (1972) and Gates (1983) who suggested a mosaic of burnt areas may benefit greater sage-grouse brood habitat. My results indicated the importance of a range of sagebrush canopy cover from 5 -12% for brood-rearing. More research is required to estimate the size of openings in sagebrush and their frequency across the landscape.

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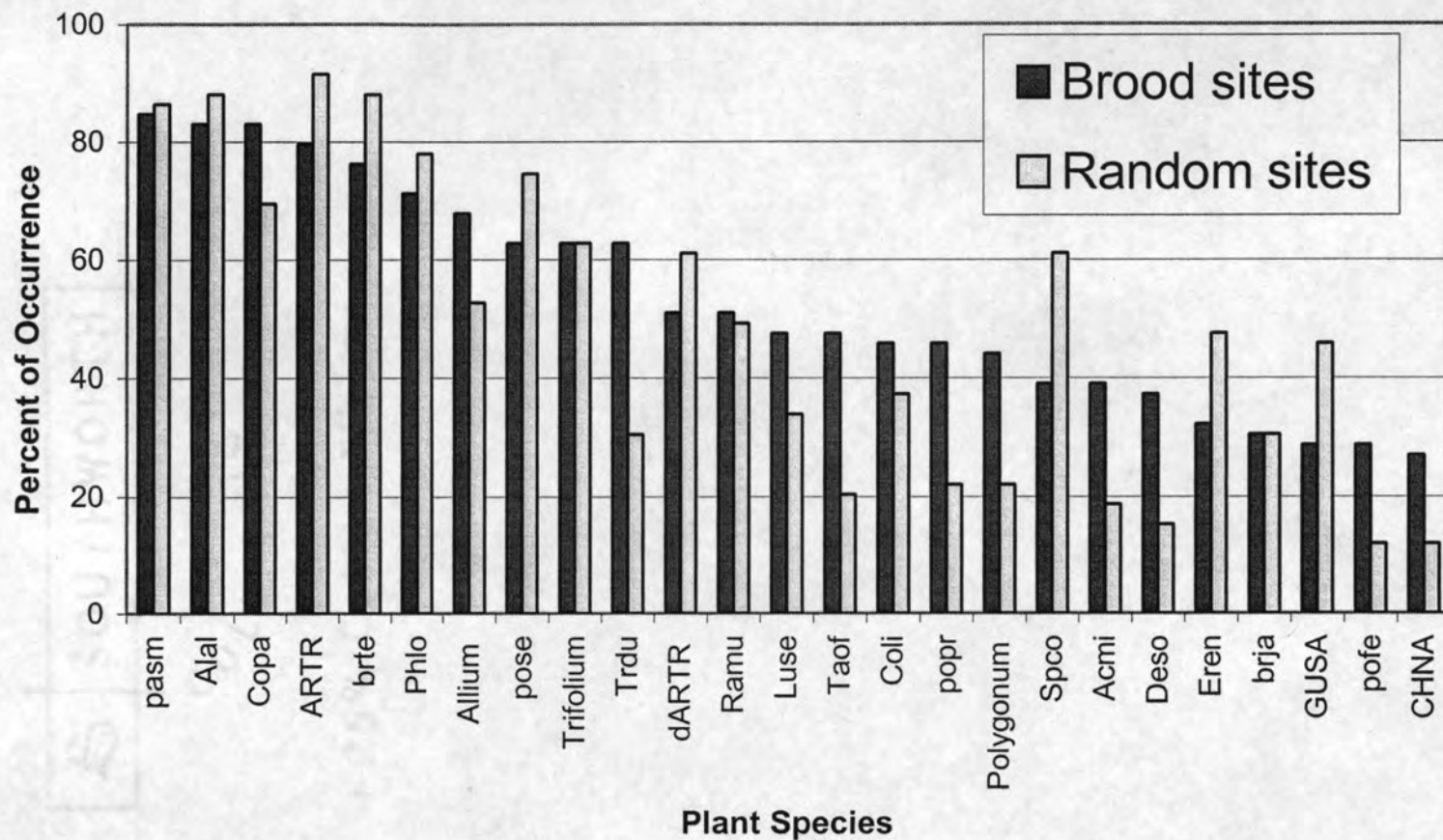


Figure 3.1. The 25 most common plant species at greater sage-grouse brood use locations and random sites in Axial Basin and Danforth Hills, Colorado, 2001. Shrubs are 4-letter genus/species code in capitals, grasses are 4-letter genus/species codes in all lower case, and forbs are 4-letter genus/species code with the first letter capitalized. Scientific names, common names and native status are found in Appendix 1-A.

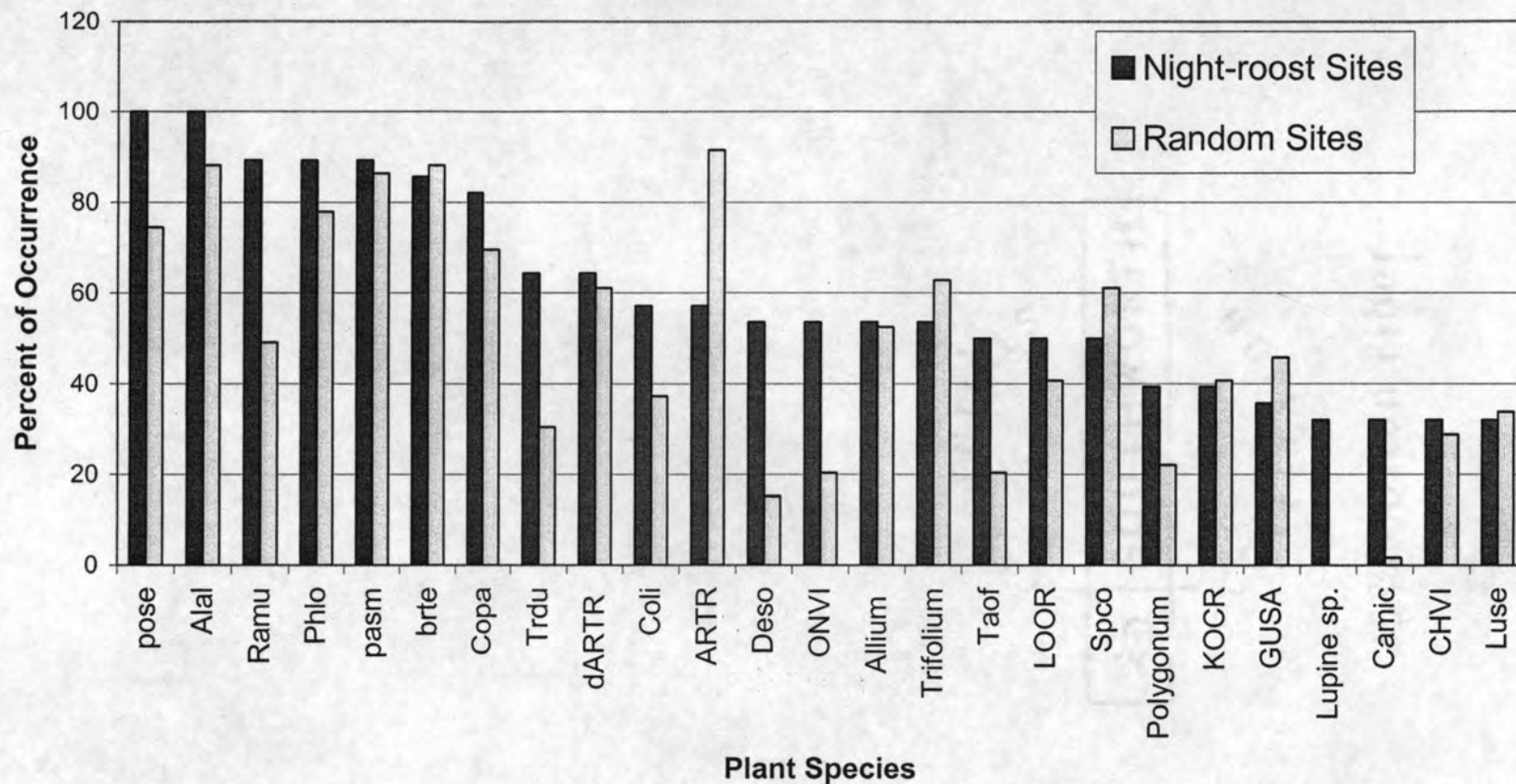


Figure 3.2. The 25 most common plant species at greater sage-grouse night-roost locations and random sites in Axial Basin and Danforth Hills, Colorado, 2001. Shrubs are 4-letter genus/species code in capitals, grasses are 4-letter genus/species codes in all lower case, and forbs are 4-letter genus/species code with the first letter capitalized. Scientific names, common names and native status are found in Appendix 1-A.

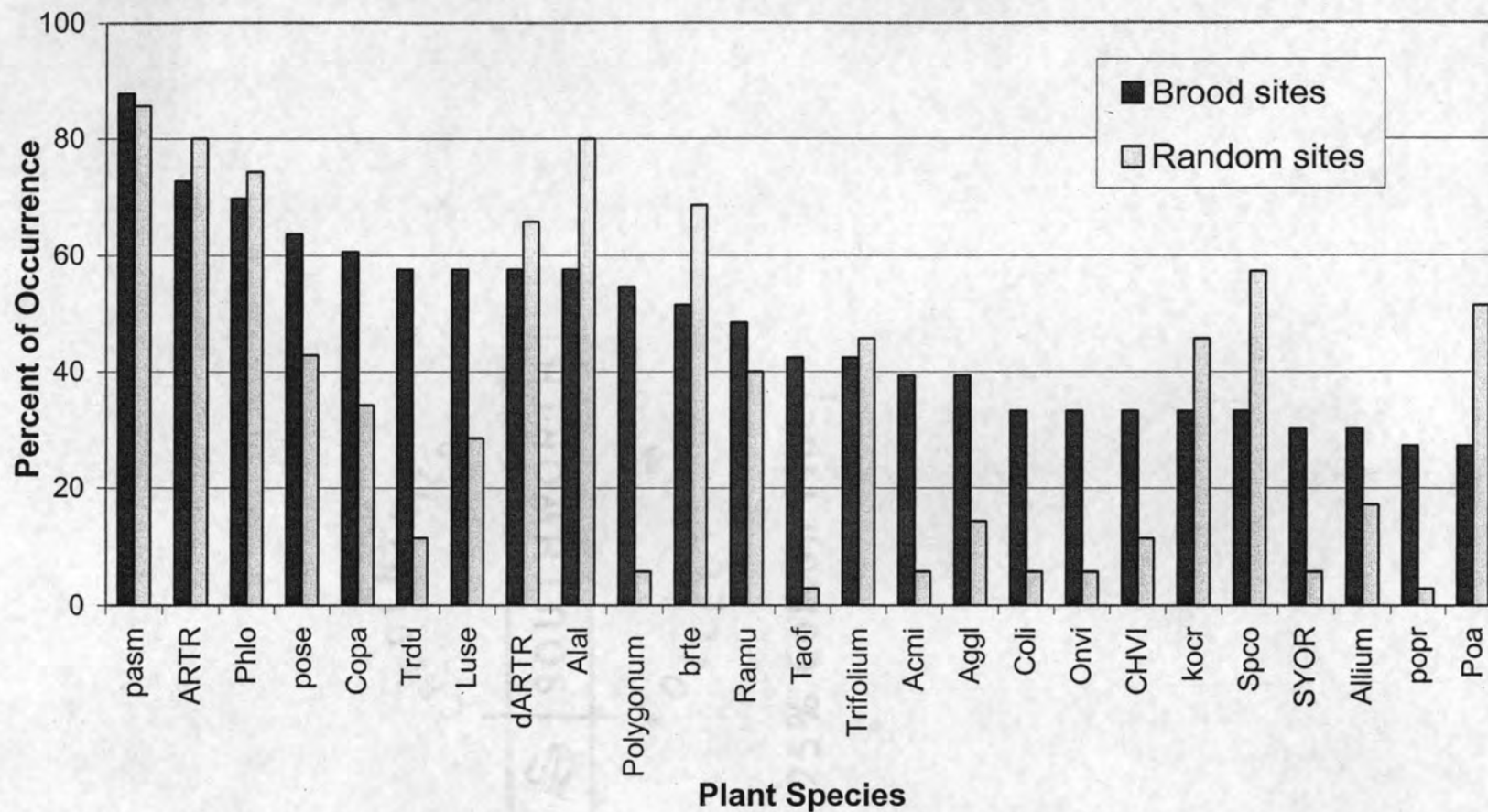


Figure 3.3. The 25 most common plant species at greater sage-grouse brood use locations and random sites in Axial Basin and Danforth Hills, Colorado, 2002. Shrubs are 4-letter genus/species code in capitals, grasses are 4-letter genus/species codes in all lower case, and forbs are 4-letter genus/species code with the first letter capitalized. Scientific names, common names and native status are found in Appendix 1-A.

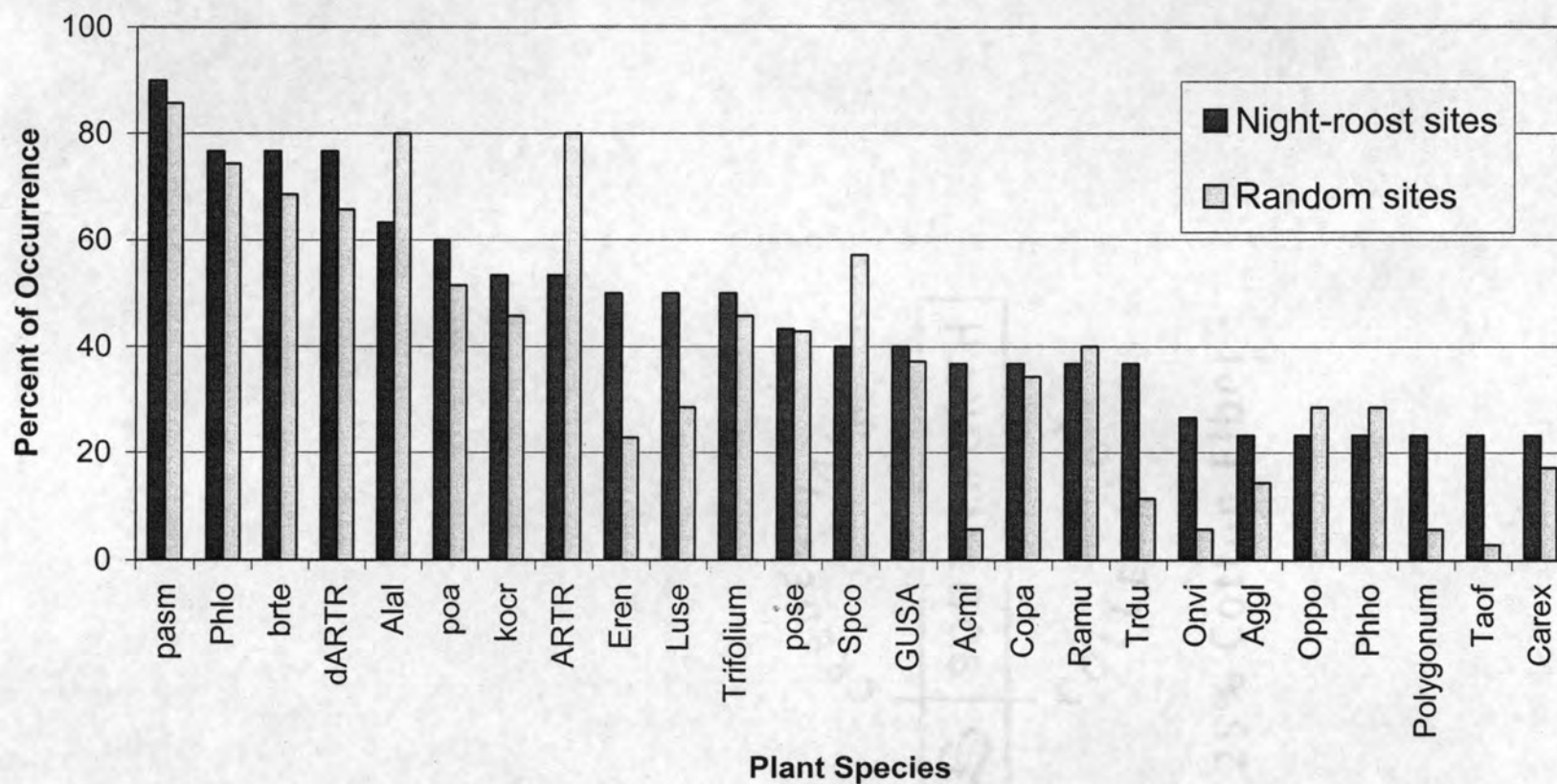


Figure 3.4. The 25 most common plant species at greater sage-grouse night-roost locations and random sites in Axial Basin and Danforth Hills, Colorado, 2002. Shrubs are 4-letter genus/species code in capitals, grasses are 4-letter genus/species codes in all lower case, and forbs are 4-letter genus/species code with the first letter capitalized. Scientific names, common names and native status are found in Appendix 1-A.

Table 3.1. Results of the multiple regression model using structural habitat variables to predict flock size of greater sage-grouse females and broods at night-roost locations during summer in Moffat County, Colorado, 2001/2002.

Dependant Variable	Parameter Estimate	Regression Coefficient (SE)	F-value	P-value	Partial r^2
Intercept	6.5	0.9	52.7	<0.001	
Visual obstruction 0- 0.5 m read from a height of 0.5 m and a distance of 5.0 m	-3.6	1.5	5.6	0.021	0.06
Visual obstruction 0.5- 1.0 m read from a height of 0.5 m and a distance of 10.0 m	4.7	1.5	9.6	0.003	0.09

Table 3.2. Results of chi-squared tests among physical macrohabitat characteristics (means and standard error) measured at greater sage-grouse brood, nocturnal and random sites in northwest Colorado, 2001/2002.

Habitat Variable	Slope	Aspect		Elevation (m)		Distance to nearest visible structure (m)	Distance to nearest two-track (m)
Year	Pooled	2001	2002	2001	2002	Pooled	Pooled
Random (<i>n</i> =93)	4.7 (0.5)	180 (15)	215 (20)	2008 (14)	1978 (17)	410.4 (123.7)	179.2 (15.5)
Brood (<i>n</i> =92)	5.3 (0.6)	147.0 (18.6)	188.0 (25.3)	2072 (19)	2117 (23)	306.5 (128.8)	163.0 (14.1)
P-value	0.077	0.001	0.097	0.002	0.373	0.862	0.112
Years	Pooled	Pooled		Pooled		Pooled	Pooled
Random (<i>n</i> =93)	4.7 (0.5)	193 (12)		1997 (11)		410.4 (123.7)	179.2 (15.5)
Nocturnal (<i>n</i> =58)	4.9 (0.6)	219 (17)		2110 (16)		383.1 (27.5)	N/a
P-value	0.183	0.007		< 0.001		0.930	N/a
Years	Pooled	2001	2002	2001	2002	Pooled	Pooled
Brood (<i>n</i> =92)	5.3 (0.6)	147 (19)	188 (25)	2072 (19)	2117 (23)	306.5 (128.8)	163.0 (14.1)
Nocturnal (<i>n</i> =58)	4.9 (0.6)	192 (27)	245 (20)	2113 (22)	2108 (24)	383.1 (27.5)	N/a
P-value	0.941	0.185	0.231	0.008	0.996	0.994	N/a

Table 3.3. Microhabitat characteristics varying between years at random sites (mean and standard error) in Axial Basin and Danforth Hills, Colorado, 2001/2002.

Habitat variable	2001	2002	F-value	P-value
Species richness	18.2 (0.7)	11.7(1.0)	29.7	<0.001
Percent forb cover	4.6 (0.3)	2.5 (0.4)	16.6	<0.001
Percent exotic cover	38.1 (2.7)	26.7 (3.8)	4.4	0.038
Percent bare ground	24.7 (3.0)	15.6 (2.8)	4.1	0.047
Visual obstruction from 5 m	18.5 (2.0)	11.5 (1.9)	5.8	0.018
Visual obstruction from 10 m	29.2 (2.1)	17.4 (2.1)	14.1	<0.001
Visual obstruction from 2.5 m (0.5-1.0 m)	9.7 (1.6)	5.9 (1.8)	4.2	0.045

Table 3.4. Pattern of 4 principal components derived from analysis of 15 microhabitat variables from 94 random plots in Axial Basin and Danforth Hills, Colorado, 2001/2002.

Structural Feature	PC1	PC2	PC3	PC4
Percent shrub cover	0.254		-0.250	0.368
Percent sagebrush cover	0.252		-0.344	
Shrub height	0.255			
Forb height		0.581		
Grass height		0.266	0.314	0.507
Percent grass cover		0.514		
Percent litter cover		-0.343		
VISOBa11 ^a	0.278		-0.309	
VISOBa22 ^a	0.311		0.302	
VISOBa23 ^a	0.306			
VISOBb11 ^a	0.282			-0.404
VISOBb12 ^a	0.306		-0.266	
VISOBb13 ^a	0.292		-0.287	
VISOBb21 ^a	0.238		0.271	-0.441
VISOBb22 ^a	0.305		0.364	
VISOBb23 ^a	0.304		0.295	
Eigenvalue	7.8	2.1	1.4	1.1
Percent of variation explained	48.7	13.4	8.5	7.2
Cumulative percent	48.7	62.1	70.1	77.8

^a Visual obstruction readings where the letter responds to reading height (a = 0.5 m, b = 1.5 m), the first number responds to the 50cm demarcations on the pole (1 = 0 m- 0.5 m, 2 = 0.5 m- 1.0 m) and the second number responds to reading distance from the pole (1 = 2.5 m, 2 = 5.0 m, 3 = 10 m).

Table 3.5. Logistic regression models of habitat variables predicting the binary variables for random and greater sage-grouse brood or night-roost sites and diurnal and nocturnal sites in northwest Colorado 2001/2002.

Dependant Variable	Parameters	Regression Coefficient (SE)	Wald χ^2	df	P
Brood/ Random	Percent forb cover	31.7 (7.0) ^a	20.5	1	< 0.0001
	Percent bare ground	-3.7 (1.3) ^a	8.6	1	0.0033
	VISOBa12 ^b	0.8 (0.3)	9.9	1	0.0016
	VISOBa13 ^b	-0.7 (0.2)	7.6	1	0.0058
Night-Roost/ Random	Percent forb cover	14.5 (6.9) ^a	4.5	1	0.0343
	Percent bare ground	-2.9 (1.1) ^a	6.6	1	0.0105
	VISOBa12 ^b	-0.9 (0.4)	4.5	1	0.0332
	VISOBa13 ^b	-0.4 (0.2)	2.8	1	0.0966
Nocturnal/ Diurnal	PC 1	-0.7 (0.2)	15.8	1	< 0.0001
	Percent exotics	-2.2 (1.1) ^a	4.4	1	0.0355
	VISOBa12 ^b	-1.5 (0.3)	21.1	1	< 0.0001

^a Arcsin transformed values

^b Visual obstruction readings where the letter responds to reading height (a = 0.5 m, b = 1.5 m), the first number responds to the 50cm demarcations on the pole (1 = 0 m- 0.5 m, 2 = 0.5 m- 1.0 m) and the second number responds to reading distance from the pole (1 = 2.5 m, 2 = 5.0 m, 3 = 10 m).

Table 3.6. Mean and standard error (SE) for habitat variables measured at greater sage-grouse brood, night-roost and random sites in Axial Basin and Danforth Hills, Colorado, 2001/2002.

Variable	Brood (n=92)	SE	Night Roost (n=58)	SE	Random (n=94)	SE
Percent shrub cover ^a	22.4	1.7	9.5	1.3	20.9	1.6
Percent sagebrush cover ^a	10.6	1.2	4.4	1.0	14.4	1.4
Shrub height (cm)	58.1	4.1	30.5	2.7	44.0	2.3
Forb height (cm)	11.2	0.7	7.6	0.4	8.2	0.5
Grass height (cm)	20.3	0.8	15.2	0.6	17.1	0.7
Percent grass cover ^a	6.5	0.6	4.9	0.4	5.9	0.8
Percent forb cover ^a	8.0	0.7	5.4	0.6	3.8	0.3
Percent exotics ^a	37.4	2.4	27.0	2.6	33.9	2.3
Percent bare ground ^a	10.2	1.2	9.1	2.1	21.3	2.2
Litter ^a	84.8	1.6	80.7	2.2	75.8	2.4
VISOBa11 (cm) ^b	16.3	1.2	3.1	0.9	12.0	1.3
VISOBa12 (cm) ^b	22.2	1.3	4.0	0.9	15.9	1.4
VISOBa13 (cm) ^b	27.9	1.4	9.6	1.6	24.8	1.6
VISOBa22 (cm) ^b	8.8	1.1	1.4	0.6	5.4	1.1
VISOBa23 (cm) ^b	12.5	1.2	2.1	0.9	8.3	1.2
VISOBb11 (cm) ^b	11.5	1.0	0.6	0.3	7.7	1.2
VISOBb12 (cm) ^b	18.5	1.3	2.2	0.7	13.5	1.4
VISOBb13 (cm) ^b	26.4	1.4	6.3	1.3	20.2	1.5
VISOBb21 (cm) ^b	3.0	0.6	0.5	0.3	2.0	1.5
VISOBb22 (cm) ^b	5.7	0.8	0.3	0.2	3.3	0.8
VISOBb23 (cm) ^b	9.5	1.2	1.1	0.7	5.1	1.0

^a Arcsin transformed for MANOVA, untransformed mean and SE are reported

^b Visual obstruction readings where the letter responds to reading height (a = 0.5 m, b = 1.5 m), the first number responds to the 50cm demarcations on the pole (1 = 0 m- 0.5 m, 2 = 0.5 m- 1.0 m) and the second number responds to reading distance from the pole (1 = 2.5 m, 2 = 5.0 m, 3 = 10 m).

Table 3.7. Microhabitat characteristics varying among early and late brood-rearing sites (mean and standard error) of greater sage-grouse in Axial Basin and Danforth Hills, Colorado, 2001. Brood-rearing periods were estimated as the time in which 90% of movements had been made to alternative cover types or long distances movements had ceased. In 2001 this date was 7 July.

Variable	Early brood-rearing (n=31)	SE	Late brood-rearing (n=28)	SE	Within Canonical
Percent shrub cover ^a	20.3	2.6	21.5	2.7	0.094
Percent sagebrush cover ^a	12.7	1.8	8.4	1.4	0.271
Shrub height (cm)	53.9	5.8	53.0	4.0	0.146
Forb height (cm)	11.1	0.8	11.3	0.9	0.122
Grass height (cm)	21.7	1.0	20.0	1.1	-0.018
Percent grass cover ^a	5.8	0.5	9.1	1.8	0.149
Percent forb cover ^a	7.5	0.7	8.9	1.0	-0.214
Percent exotics ^a	40.9	4.6	37.7	3.1	0.118
Percent bare ground ^a	14.0	2.8	9.9	1.5	0.003
Litter ^a	77.9	4.2	87.6	1.2	-0.121
VISOBa11 (cm) ^b	16.5	2.0	16.1	2.6	0.116
VISOBa13 (cm) ^b	32.3	2.2	31.4	2.3	0.133
VISOBa21 (cm) ^b	3.7	1.5	5.3	1.5	0.091
VISOBa23 (cm) ^b	12.5	2.5	15.4	2.1	0.192
VISOBb11 (cm) ^b	12.6	1.8	11.5	1.8	0.233
VISOBb13 (cm) ^b	28.1	2.0	26.8	2.4	0.200
VISOBb21 (cm) ^b	3.0	1.2	2.6	0.9	0.176
VISOBb23 (cm) ^b	8.3	2.1	10.3	2.0	0.209

^a Arcsin transformed for MANOVA, untransformed mean and SE are reported

^b Visual obstruction readings where the letter responds to reading height (a = 0.5 m, b = 1.5 m), the first number responds to the 50cm demarcations on the pole (1 = 0 m- 0.5 m, 2 = 0.5 m- 1.0 m) and the second number responds to reading distance from the pole (1 = 2.5 m, 2 = 5.0 m, 3 = 10 m).

CHAPTER 4. SEASONAL AND ANNUAL MOVEMENTS AND SURVIVAL OF GREATER SAGE-GROUSE IN NORTHWEST COLORADO

INTRODUCTION

The life history of greater sage-grouse has been relatively well studied (Schroeder et al. 1999) and many studies have monitored radio-marked individuals. Despite this, there are shortcomings in the reports of annual and seasonal survival rates and home ranges across the range of greater sage-grouse. Large-scale survival studies have been limited to mark-recapture data from banded individuals or have not provided seasonal estimates, confidence limits or annual comparisons (Connelly et al. 1994, Zablán et al. 2003). Home range analysis in the literature has been limited to a few radio-marked individuals describing brood home range, and no data are available estimating annual home range sizes.

Home range is an area used by an individual in its normal daily activities (Burt 1943). Brood home range is the area maintained by a brood from hatch until 10 weeks, when brood identity is lost and chicks are considered independent (Wallestad 1971, N. Burkepile personal communication). Home range size and movements are widely used in wildlife biology to assess animal-habitat relationships and survival (Thompson and Fritzell 1989, White and Garrott 1990, Drut et al. 1994, Chamberlain and Leopold 2000). However, home range estimation can be influenced by autocorrelated data (Otis and White 1999), sample size and the home range estimator used (Girard et al. 2002). The validity and utility of applying results of home range analysis to long-term wildlife management objectives also depends on the assumption that populations remain faithful to such ranges over time (Van Dyke et al.

1998). Greater sage-grouse females exhibit site fidelity to leks (Dunn and Braun 1985), nest sites (Fisher et al. 1993) and winter areas (Berry and Eng 1985).

Understanding the dynamics of a wild population requires precise estimates of annual survival (Zablan et al. 2003). My objectives were to (1) estimate seasonal and annual movements, (2) estimate monthly, seasonal and annual survival rates by age class and (3) to develop predictive seasonal and annual survival models of females using years, seasons, age and trend as covariates.

METHODS

Movements were separated into 4 periods for analysis: breeding (16 March -15 June), brood-rearing (15 June - 31 August), fall (1 September - 15 November) and winter (16 November - 15 March), based on grouse behavior. The lek of capture served as the point of origin for all grouse captured on lek sites and the initial nest site was the ending point for breeding season movement, thus analysis was restricted to females that initiated nests. Distances were estimated using ARCVIEW. Mean distances to nests following a nest success between years and a failure in the same year were compared using a student's t-test. Lek to nest distance was related to female age, location of lek, and year using ANOVA. Mean distances moved by yearling and adult females seasonally and annually were compared using an ANOVA (Ott and Longnecker 2001).

Seasonal Movements

For fall and winter seasons, I estimated the mean movement of individual grouse from the lek or site of capture and then derived the overall mean movement per season from the averages to take into account discrepancy in number of locations per bird. Grouse with <

3 locations/ season were not included in the analysis. Fall and winter movements were log transformed to meet the assumption of normality and then assessed for variation between ages, and years using ANOVA. Movement directions and altitudinal migration was estimated using ARCVIEW.

Daily Movements

Seasonal home range and median daily movement were restricted to the brood-rearing season, as consecutive locations in the fall and winter were too far apart in time (Samuel and Fuller 1996). Linear distances were calculated between subsequent locations and divided by the number of days elapsed between locations. A regression analysis was used to estimate the influence of daily movement on number of chicks/female at 6 weeks post-hatch. Daily movements did not meet the assumption of normality therefore I used a non-parametric Kruskal-Wallis ANOVA to evaluate differences between ages, years and brood status (successful vs. unsuccessful females). Median distances moved to night-roost sites were calculated for females whose diurnal location was < 12 hrs before or after the night-roost site.

Home range

An ARCVIEW extension, Animal Movement (Hooze and Eichenlaub 1997) was used to estimate home range sizes. Independent locations (≥ 24 hrs apart) were used in the calculations. A 95% fixed kernel estimate of home range was used with least squares cross-validation to choose the width of kernel bands. This estimator is considered accurate even with < 20 locations, and is not biased by an unequal number of locations (Seaman et al. 1999). Brood home ranges (hatch to 10 weeks) from 2001 and 2002 were pooled because samples from each year were too small for statistical analysis. I used a non-parametric

Kruskal-Wallis ANOVA to evaluate differences in brood home range size with respect to nest location and age. Annual home range estimates were evaluated for females that survived annually and had > 20 independent locations (range 21- 40) using a non-parametric ANOVA to estimate differences due to year or age.

Survival

Female survival was analyzed using program MARK (White and Burnham 1999), which incorporated Kaplan-Meier product limit method with staggered entry (Pollock et al. 1989). Monthly, seasonal and annual survival rates for yearlings and adults were calculated. The annual survival interval commenced 1 April. Grouse classified as yearlings at the time of capture were re-classified as adults the following April. After building the global model, the data were analyzed for overdispersion, a phenomena which reflects the lack of independence or heterogeneity among individuals (Anderson et al. 1994). A $\hat{c} > 1$ indicates that the data are heterogeneous and dependent. I calculated $\hat{c} = 2.43$ for the annual data, indicating that the gregarious nature of greater sage-grouse year-round caused individuals to be interpreted as units. Overdispersion was not seen in the seasonal analysis ($\hat{c} < 0.77$). The annual data set was corrected for overdispersion and models were selected using the small sample bias corrected quasi-Akaike's Information Criteria (QAICc). The small sample-bias corrected Akaike's Information Criteria (AICc) was used to select among seasonal models. The principle of parsimony was used to select the best model among alternative parametric models (Burnham and Anderson 1998). Models were selected to determine whether survival rates differed among season, between years or age classes (Pollock et al. 1989). Individuals were recovered as soon as possible after a mortality signal was heard. Cause-specific

mortality was classified as avian, mammalian, or unknown through examination of the carcass and surrounding area (S. Boutin, personal communication).

RESULTS

Seasonal Movements

Mean lek to nest movements for 2001 (4.00 km, $SE = 0.56$, $n = 41$) did not differ ($F = 0.17$, 1 df , $P = 0.682$) from 2002 (4.01 km, $SE = 0.46$, $n = 60$). Mean lek to nest movements for females attending leks in the Axial Basin (4.58 km, $SE = 0.45$, $n = 72$) was larger ($F = 6.74$, 1 df , $P = 0.011$) than that of females attending leks in the Danforth Hills (2.59 km, $SE = 0.43$, $n = 29$). Average lek to nest movements for adults (3.90 km, $SE = 0.42$, $n = 72$) was similar ($F = 0.26$, 1 df , $P = 0.613$) to that of yearlings (4.31 km, $SE = 0.69$, $n = 26$).

The average distance adult females moved between consecutive nests either between years or to reneest was 0.45 km ($n = 25$). The mean distance females moved to consecutive nests following a successful nesting attempt was 0.32 km, $SE = 0.09$, $n = 13$, which did not differ ($t = 1.34$, $P = 0.190$) from the distance moved following a nest failure to reneest or between years (0.58 km, $SE = 0.18$, $n = 12$).

Mean female movement in the fall from the lek of capture was 7.8 km (range: 0.4 – 21.5 km, $n = 70$) and did not vary between ages ($F = 0.03$, $P = 0.874$) or years ($F = 0.00$, $P = 0.955$). Mean movement from winter locations to leks was 9.9 km (range: 0.8 - 30.6 km, $n = 76$) and also did not vary between ages ($F = 0.02$, $P = 0.893$) or years ($F = 0.27$, $P = 0.608$). Seasonal movements tended to be elevational in nature. Directional movements of females was northwest to winter sites < 1,978 m in the Axial Basin. Some females moved further northwest to winter home ranges between Lay and Sunbeam, Colorado. Female movement was from mid-October to mid-November and then grouse remained at low elevations until

mid-March. Movements to leks occurred from mid-March to early April. Elevation of females during the breeding season ranged from 2,045 – 2,090 m. Another movement upward in elevation ($> 2,100$ m) was observed in July and August (Figure 4.1).

Daily Movements

I collected 1,103 greater sage-grouse locations over the brood-rearing period. Of these locations, 92% were collected within 10 days of the previous location. Individuals with < 3 locations and location > 10 days apart were excluded from analysis (Apa 1998). For females with broods ($n = 23$), the greatest daily movements were made in weeks 6 and 7 post-hatch. I detected no difference in daily movement by year ($\chi^2 = 1.82$, $P = 0.179$) or age of female ($\chi^2 = 0.67$, $P = 0.412$). A difference was detected, however, for brood status. Females with broods (median: 184 m/day, range = 15 - 520, $n = 50$) moved further ($\chi^2 = 25.53$, $P < 0.001$) than those without (median: 103 m/day, range = 46 - 566, $n = 47$). Brood size at 6 weeks post-hatch was not associated with daily movements ($F = 0.06$, $P = 0.813$, $r^2 = 0.001$, $n = 50$). Median movement from the most recent day locations (< 12 hrs) to night roost locations was 397 m, range: 77 – 4,462 m.

Home range

The distributions of brood and annual home range sizes were skewed so the median was used to determine the central tendency of the data (Ott and Longnecker 2001). An outlier, with home range of 8,176 ha was removed from analysis of brood home range. No differences were detected between brood home range sizes of adults and yearlings ($\chi^2 = 0.13$, 1 *df*, $P = 0.721$). However, home range sizes of brood females that nested in the Axial Basin (1,151 ha) were larger ($\chi^2 = 3.69$, 1 *df*, $P = 0.055$) than those that nested in the Danforth Hills (439 ha) (Table 4.1). Annual home range estimates did not vary between years ($\chi^2 = 0.04$, 1

df , $P = 0.850$). Median annual home range of yearling females was 8,574 ha, $n = 26$ and did not differ ($\chi^2 = 0.0001$, 1 df , $P = 0.990$) from that of adult females (6,556 ha, $n = 43$) (Table 4.2).

Survival

Annual survival rates for adult females were 0.65, and 0.48 for 2001 and 2002, respectively (Table 4.3). Annual survival rates were 0.71 and 0.78 for yearling females. Annual survival rates pooled over 2 years were 0.75 for yearling females and 0.57 for adult females. Seasonal survival rates were lowest in the brood-rearing period in 2001 and the breeding period for 2002. Survival for the brood-rearing period (16 June - 31 August) in 2001 was 0.84 for adult females and 0.85 for yearling females, while survival for the breeding period (1 April - 15 June) in 2002 was 0.75 for adult and 0.84 for yearling females (Table 4.3).

Monthly survival rates in 2001 were lowest for both adult (0.88) and yearling (0.88) females in July (Tables 4.4 and 4.5). In 2002, however, monthly survival rates were lowest in May (0.85) and October (0.85) for adult females and May, June and September and October (0.93) for yearling females. November through March were periods of low mortality for females in both years (Tables 4.4 and 4.5).

Models were constructed to determine whether seasonal survival rates varied with year or age. In model building, $\{S(t)\}$ denotes variation due to year and $\{S(a)\}$ denotes variation due to age. The model $\{S(a + t)\}$ denotes variation due to both parameters. Models within a ΔAIC_c of ≤ 2 showed insufficient evidence to be excluded as the most credible model. $AIC_c > 2$ Δ but ≤ 4 , provided weak evidence that the model was not the best. Models with $\Delta AIC_c > 4$ but ≤ 7 , exhibited strong evidence that the model was not the best fit

for the data (Burnham and Anderson 1998). The model that best fit the data for breeding-period survival was the model $\{S(a + t)\}$, which indicated that survival varied between ages and years (Table 4.6). For the brood-rearing, fall, and winter seasons the model that best fit the data was the null model, indicating that survival did not vary by age or year (Table 4.6). The annual survival models selected were the null model and survival that varied with age, year and seasonal trend (Figure 4.2). Based on the principle of parsimony, the null model was considered the best of the competing models (Table 4.7).

Length of time between the last alive signal and carcass retrieval for greater sage-grouse averaged 10.46 days. Through examination of carcasses retrieved within 5 days ($\bar{x} = 2.5$, $n = 18$), I attributed 39% of mortalities to mammalian predation ($n = 7$), 39% unknown ($n = 7$), 17% to avian predation ($n = 3$), and 6% to reptilian predation ($n = 1$). Of the avian mortalities 1 was likely a great horned owl and the other 2 were attributed to golden eagles (*Aquila chrysaetos*). The reptile death was attributed to a Western rattlesnake bite (*Crotalus viridis*). This mortality also occurred while the female was incubating. Two puncture wounds were found on the lower abdomen and were perhaps inflicted as the female attempted to protect her eggs. Her carcass was found a short distance from the nest and her eggs were covered in blood.

Of the avian-suspected depredations retrieved within 5 days ($n = 3$), 1 was attributed to a great horned owl. The carcass was recovered at midnight during a night-roost sampling session. The transmitter had not switched to mortality, the carcass was still warm and the female had died as a result of impact to the head. The microhabitat was a wet meadow. The other 2 mortalities were attributed to avian causes because of characteristics of the kill. One had a severed head present and bones dislocated with clean breaks at the joints. Intestines

were pulled out and smeared on the remains. The microhabitat was an 8°, north-facing slope in 5-10% sagebrush canopy cover. The other avian-suspected mortality had streaks of whitewash present at the site of the collar. No other remains were found. The microclimate was a 20° south-facing slope at the edge of a rock cliff.

Of the mammalian-suspected depredations retrieved within 5 days ($n = 7$), none had whitewash, pellets, scat, raptor feathers or tracks present at the kills site. Four carcasses had blood present indicating that the kill was made at the site. Of those, 2 were females incubating nests, 1 was killed in a mountain shrub community and 1 in 5-10% sagebrush canopy cover. The head was severed at 1 kill site, and legs remained at 2 sites. Seventy-one percent of mammalian-suspected depredations had skin remaining on tufts of feathers and 43% exhibited feathers broken at the quills and the cecum present in 1 piece. Two sites had broken bones, cracked between the joints. Feathers were scattered from 1-3 m² and wings were remaining intact at 43% of kill sites. The mammalian depredations could not be distinguished to species, due to confounding evidence at all sites.

DISCUSSION

Seasonal Movements

Greater sage-grouse populations have been described as migratory or non-migratory (Eng and Schladweiler 1972, Wallestad 1975, Schoenberg 1982, Connelly et al. 1988, Leonard et al. 2000). Migration can either occur between winter/nest areas and summer areas, winter and nest/summer areas or by a combination of movements between winter, nest and summer areas (Schroeder et al. 1999).

Nesting tends to be associated with sagebrush habitat surrounding lek sites (Connelly et al. 2000b), but has also occurred > 20 km from breeding grounds (Wakkinen et al. 1992). Distances traveled from breeding grounds to nest sites in central Montana averaged 2.5 km and 2.8 km for adults and yearlings, respectively (Wallestad and Pyrah 1974). Alternatively, a study by Schoenberg (1982), in North Park, Jackson County, Colorado indicated that adult females traveled further to nests than did yearlings. Lek to nest distance averaged 2.7 km. Lek to nest movements of 4.0 km in my study is similar to those found in Idaho, which ranged from 3.4 to 4.9 km (Wakkinen 1990, Apa 1998, Fischer 1994). Lek to nest movements may be an indicator of suitable nesting habitat. Habitat in the Axial Basin was less suitable for nesting than that in the Danforth Hills (Chapter 1), thus females were required to move further from breeding grounds to nesting sites in the Axial Basin.

The mean distance to consecutive nests was 0.45 km ($n = 25$), which is less than the 0.70 km ($n = 22$) reported in Idaho (Fischer et al. 1993). Dunn and Braun (1985) speculated that nest fidelity might be related to nest success. My results failed to confirm this, as movements to successive nests did not differ based on nest fate.

Greater sage-grouse in northwestern Moffat County migrated up to 30.3 km to wintering areas in late November as reported by Dunn and Braun (1986). This is consistent with what I observed; the greatest distances moved from brood-rearing sites to fall and winter areas (30.6 km) occurred in November and December. Mean distances from the lek of capture in the fall and winter was 7.8 and 9.9 km, respectively. Dargon et al. (1942) noted elevational migration of greater sage-grouse near Craig, Colorado and in the Axial Basin. In this study movements to below 2,073 m began in mid-November and were completed by the start of December. A second migration upward in elevation began in late February and

continued on through March. I observed mean elevation of females below 2,000 m from November-March. Movement upward in elevation began in late March and continued on through August. Movements of migratory greater sage-grouse in Wyoming, Idaho and Colorado ranged from 20-82 km (Schoenberg 1982, Berry and Eng 1985, Connelly et al. 1988) between summer, winter and breeding areas. The mean movement of females between seasons from the lek of capture was < 10 km in my study, which indicates this population is non-migratory.

Daily Movements

Median daily brood movements (184 m/day) were similar to those reported by Apa (1998) (144 m/day, $n = 9$), but less than those reported by Autenrieth (1981). Previous research indicated that greater sage-grouse chicks changed their diet and subsequently their habitat use at 6 weeks of age (Martin 1970, Peterson 1970, Drut et al. 1994). This corresponded with the greatest movements being made at 6 and 7 weeks post-hatch. There was also a peak in movement of broods at 3 and 4 weeks post-hatch. This was associated with females that hatched nests late, likely re-nesters. Broods that hatched late in the season were forced to move earlier in search of forbs and insects.

Females with broods ($n = 50$) moved a distance of 80 m/day further than females without broods ($n = 47$). Broods have higher energetic demands and may require greater search times for specific food items. Contrastingly, Apa (1988) observed that females with broods (median: 144 m/day, $n = 9$) moved less than females without broods (median: 284 m/day, $n = 4$). While brood size in my study was not associated with daily movements, a study on gray partridge broods in the United Kingdom showed that survival rates were strongly negatively correlated with distances moved (Green 1984, Rands 1985). Similarly,

research on greater sage-grouse broods in Oregon related larger brood home ranges with less suitable habitat availability, and conjectured that the differences were associated with reduced reproductive potential (Drut et al. 1994).

Median movements from the most recent day locations to night-roost locations were 397 m. Similarly, Beck (1977) reported movements of individuals to winter night-roost locations from their last observed diurnal locations of > 250 m. Given that the median daily movement for brood females was only 184 m/day, and movements to night-roost locations were 2 times further, indicated that females with broods moved significant distances in order to find suitable night-roosting habitat. Additionally, this suggested that literature values of daily movements were underestimated as researchers failed to include nocturnal forays into their movement data.

Home range

Home range sizes may reflect the energy expended by an animal in searching for its basic requirements (Burt 1943). Chamberlain and Leopold (2000) found that movement in turkeys (*Meleagris galapavo*) increased with decreasing habitat quality and increasing habitat variability. Likewise, survival rates of male ruffed grouse (*Bonasa umbellus*) in central Missouri and female ring-necked pheasant in southern Wisconsin were inversely related to seasonal home range size and mean daily movement (Gatti et al. 1989, Thompson and Fritzell 1989). Alternatively, Hubbard et al. (1999) found that the risk of mortality for female turkeys decreased by 2.0% for every 10 ha increase in home range size.

Home range sizes for greater sage-grouse vary in the literature, although few data are available. Three yearling females with broods occupied a summer home range of 94 ha in southeast Idaho (Connelly and Markham 1983). Wallestad (1971) reported brood home

range sizes in central Montana to be 233 ha ($n = 13$). In Oregon, brood home range sizes were associated with less suitable habitat (Drut et al. 1994). Home range sizes from hatch to 12 weeks were 900 ha and 7,200 ha for good and poor habitat, respectively. Using this standard, our median brood home range size for 10 weeks of 548 ha ($n = 31$) implied that the habitat available was good. However, home range sizes varied significantly with nesting location in my study area. The implication is that birds that nested in the Danforth Hills (median home range = 439 ha) were required to move less in order to meet their basic needs than birds that nested in the Axial Basin (median home range = 1,151 ha). Habitat in the Axial Basin had less forb cover and more bare ground than in the Danforth Hills, attributes which made it less suitable for brood-rearing (Chapter 1).

Birds breeding in the Danforth Hills typically showed an altitudinal migration in the late brood-rearing period while females breeding in the Axial Basin either moved into the Danforth Hills or remained in riparian/wet meadows in the Axial Basin. The movement of birds in late summer in my study area is consistent with Wallestad (1971), Schoenberg (1982), and Wakkinen (1990) who noted shifts in late brood-rearing habitat to more mesic sites as forbs began to desiccate. Fischer et al. (1996) related this movement to vegetal moisture content of $\leq 60\%$ water. Most females in the study area migrated southward and upward in elevation to mountain shrub communities in the Danforth Hills (Savage 1969). However, some birds in the Axial Basin remained in wet meadow or riparian areas following a gradient of forbs (Klebenow 1969).

Leonard et al. (2000) described a 3-way movement of a migratory population of greater-sage grouse on the Upper Snake River plain of Idaho. Movements were from breeding/summer use areas to fall areas and finally to wintering sites, and encompassed

276,400 ha. Median annual home range estimates for yearlings and adults in the Axial Basin and Danforth Hills was 8,574 and 6,556 ha, respectively. No estimates are available in the literature describing annual home range size of individual greater sage-grouse, however, the annual home range sizes and seasonal distances traveled from the lek of capture indicated that the population of greater sage-grouse residing in the Axial Basin and Danforth Hills is non-migratory.

Survival

The annual survival models selected suggested that survival varied with age, year and seasonal trend. Additionally, seasonal survival models selected indicated that survival rates varied between years and ages for the breeding period and did not vary by age or year for brood-rearing, fall or winter seasons. Mean annual survival rates for adult and yearling females in the study area were 57% and 75%, respectively. Previous estimates in Moffat County, Colorado indicated female survival rates to be 60%. In Idaho, annual survival rates for females as reported by Connelly et al. (1994) ranged from 68-85%. Similarly, Zablan et al. (2003) estimated annual survival rates of adults (59%) to be less than that of yearling females (77%) from a 17-year band-recovery data set in North Park, Colorado. They indicated, however, that models incorporating time effects for each year did not fit the data as well as those that incorporated a trend over multiple years. For the breeding period, the model incorporating annual time effects was likely selected for my data set due to the disparity in precipitation over the 2-year study (Appendix 1-B). In the second year, the lowest seasonal survival rates were during the breeding period, and were greater for adult than yearling females. Of 13 mortalities in May and June 2002, 62% ($n = 8$) of these

occurred as females incubated potentially as a result of reduced herbaceous cover at the nest due to low precipitation in the spring (Chapter 1).

The survival rates and the competing annual models indicated that there was an upward trend in seasonal survival from the breeding period to the winter. This is consistent with populations in Idaho where 52% percent of adult female mortality occurred during the spring and summer and 46% occurred in September and October (Connelly et al. 2000a). This data, however, was collected on exploited greater sage-grouse populations where 42% of deaths of adult females were attributed to hunting. Additionally, Wik (2002) reported that the lowest seasonal female survival rates in southwestern Idaho occurred in the fall and associated these mortalities with harvest. Seasonal and monthly survival rates did not indicate hunting to be a factor affecting mortality of adult females in my study population. I had no documented band returns over 2 seasons of 109 radio-marked and 23 banded grouse alive in September. Birds resided in both the Danforth Hills, which is closed to hunting, and on BLM and private land in the Axial Basin during the hunting season in Moffat County. Although high monthly mortality rates were observed among yearling females in September and October, examination of carcasses indicated predation to be the main cause of mortality. Bowman and Harris (1980) indicated cover strongly influenced prey vulnerability. Typical canopy cover for nesting females is less than that at brood-rearing sites (Schoenberg 1982). A biological explanation for low survival during the breeding season, particularly in a drought year, was that incubating females were immobile and had poor concealment due to stunted herbaceous growth. Grass heights were 6-7 cm shorter and there was 30% less vertical and 25% less horizontal cover at the nest bowl in 2002 (Chapter 1). Additionally, low survival rates occurred in July, during the brood-rearing period. In this period, as the

vegetation desiccated, grouse made their greatest movements related to vegetal moisture content (Fischer et al. 1996). Additionally, female survival was low in October, the time when females were making their movements to winter sites. Females in the Axial Basin and Danforth Hills underwent the same trends as those in southern Idaho, and experienced low mortality over the winter (Connelly et al. 2000a).

Cause-specific mortality was primarily mammalian, although, using marks on the transmitter as a diagnostic tool, I may have over-estimated this cause of mortality. Bumann and Stauffer (2002) argued that survival studies reporting cause-specific mortality typically overestimated mammalian-caused mortality due to scavenging of the carcass. By analyzing remote cameras at ruffed grouse carcasses in Virginia, they estimated 100% of carcasses were scavenged in > 5 days. They indicated that marks to the transmitter can serve as a diagnostic when determining cause of death, as mammalian predators tended to focus on the head and neck when killing avian prey. Using this time criteria, 71% ($n = 5$) of mortalities attributed to mammalian causes may be false as there were no marks on the transmitter.

MANAGEMENT IMPLICATIONS

Survival rates for the population of greater sage-grouse in the Axial Basin and Danforth Hills appeared to be consistent with or higher than literature values in years of normal precipitation. Cause-specific mortality appeared to be primarily mammalian, although a high proportion of these may have been false due to misinterpretation of remains due to scavenging. In order for a cause-specific mortality study to be of greater value, the time from death to carcass recovery needs to be reduced and the rate of scavenging of greater sage-grouse carcasses in a shrub-steppe community needs to be estimated through the use of

remote cameras (Bumann and Stauffer 2002). Because nest success appeared high, chick survival (Chapter 3) and juvenile survival needs to be examined as mechanisms limiting this population (Connelly and Braun 1997, Connelly et al. 2000b).

Nest site fidelity in this population appears to be higher than reported in other studies. Nest fidelity can result in reduced nesting if large tracts of nest habitat are destroyed (Fischer et al. 1993), thus emphasizing the importance of nest habitat identification and conservation.

The exaggerated movements females made to night-roost habitat within the context of daily brood movements may have indicated that this habitat type may have been limited during the summer. Habitat features are involved in determining the vulnerability of prey and are exaggerated under drought conditions (Reynolds et al. 1988). Habitat conditions appeared to be inversely related to movement and directly associated with survival. Further research is needed to explore how different land use practices might improve habitat conditions for nesting and brood-rearing in the Axial Basin and whether increasing the frequency of burned areas on the landscape would decrease movements to nocturnal use sites.

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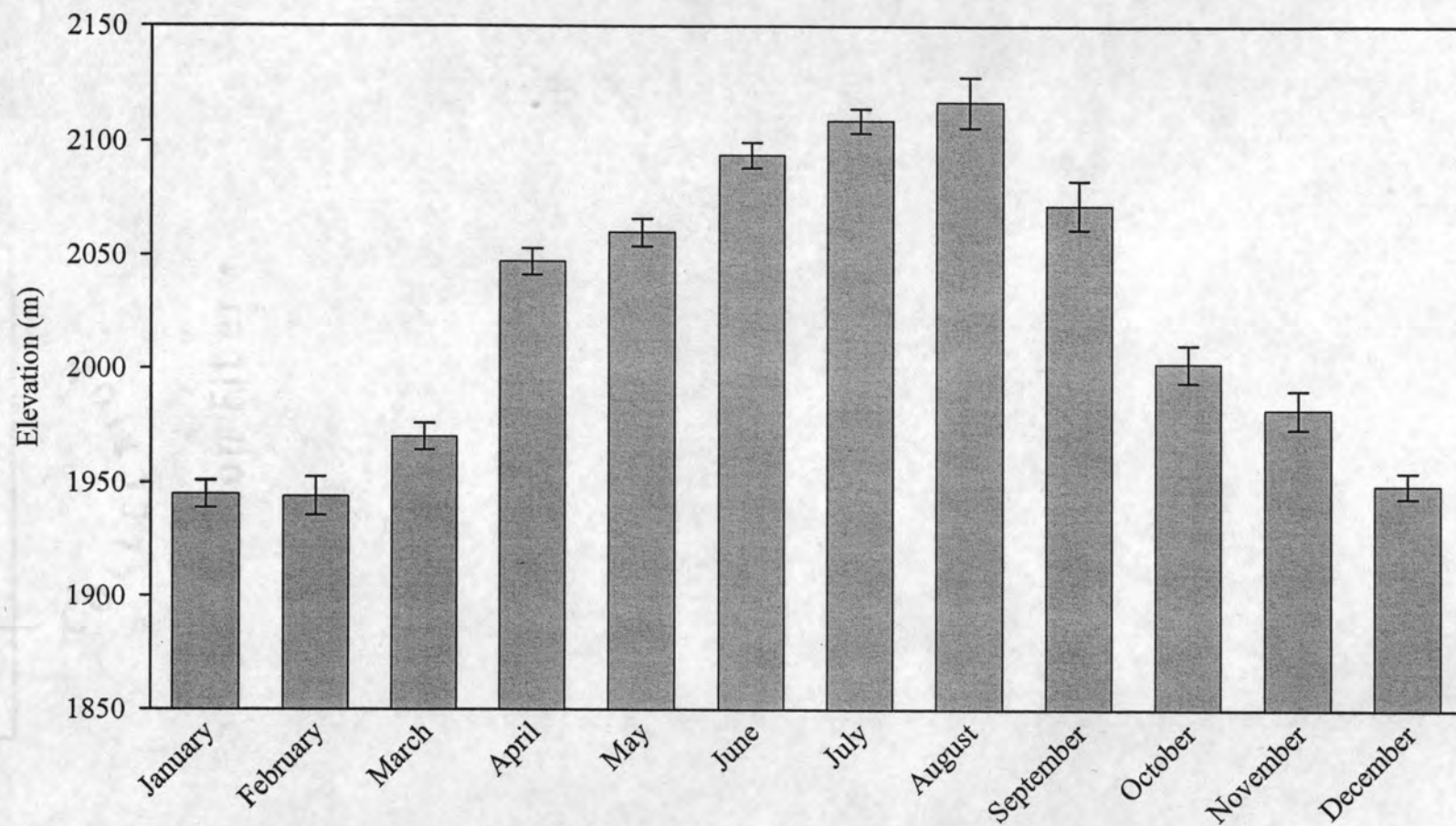


Figure 4.1. Mean monthly elevation and standard error of radio-marked greater sage-grouse females in the Axial Basin and Danforth Hills, Colorado in 2001 and 2002.

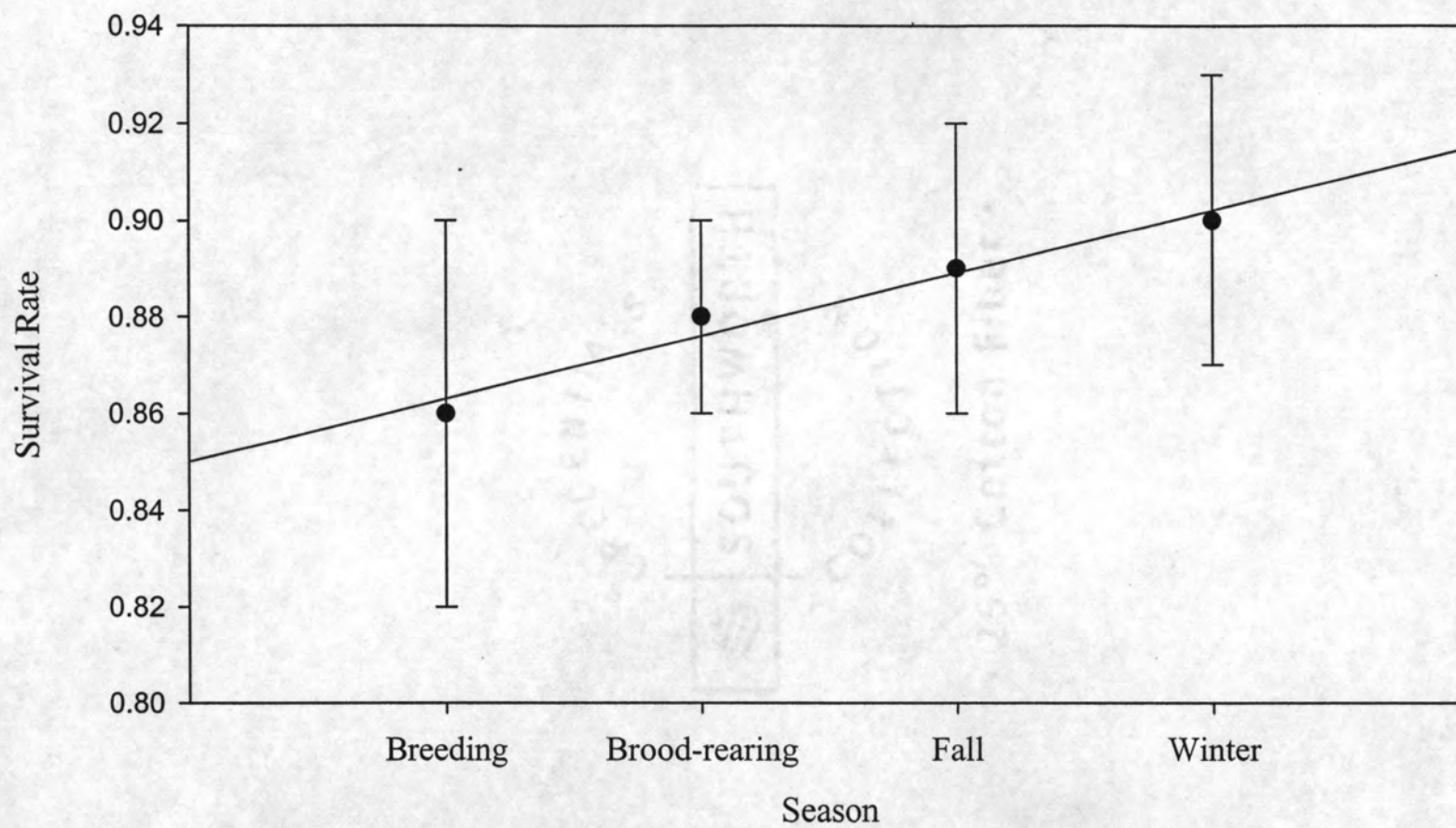


Figure 4.2. Annual survival model $\{S(T)\}$, time trend in seasonal survival of greater sage-grouse females in the Axial Basin and Danforth Hills, Colorado in 2001 and 2002. Survival rates and standard errors reported.

Table 4.1. Median home-range estimates (95% fixed kernel, with least squares cross-validation) and 95% confidence intervals around the median of greater sage-grouse brood-rearing females in northwest Colorado, 2001-2002.

Category	<i>n</i>	Median (ha)	Lower CI (95%)	Upper CI (95%)	Range
Axial Basin females	15	1,151	199	3,334	470 - 4,186
Danforth females	14	439	160	1,129	124 - 1,581
Yearlings	7	470	*	*	124 - 4,186
Adults	22	543	199	1,379	135 - 3,343

* No confidence interval at this *n* exists

Table 4.2. Median annual home-range estimates (95% fixed kernel, with least-squares cross validation) and 95% confidence intervals around the median of greater sage-grouse females in northwest Colorado, 2001/2002 and 2002/2003.

Category	n	Median (ha)	Lower CI (95%)	Upper CI (95%)	Range
Yearling	26	8,574	3,129	12,959	648 – 21,533
Adult	43	6,556	4,277	11,554	1,249 - 61,544

Table 4.3. Annual and seasonal survival rates of radio-marked greater sage-grouse females in northwest Colorado 2001 and 2002.

	Season	Survival Rates	Standard Error
2001/2002 Adult ($n = 35$)	Breeding	0.91	0.05
	Brood-rearing	0.84	0.06
	Fall	0.89	0.06
	Winter	0.96	0.04
	Annual	0.65	0.08
Yearling ($n = 27$)	Breeding	0.96	0.04
	Brood-rearing	0.85	0.07
	Fall	0.95	0.04
	Winter	0.90	0.06
	Annual	0.71	0.09
2002/2003 Adult ($n = 59$)	Breeding	0.75	0.06
	Brood-rearing	0.93	0.04
	Fall	0.90	0.05
	Winter	0.82	0.07
	Annual	0.48	0.07
Yearling ($n = 18$)	Breeding	0.84	0.08
	Brood-rearing	0.94	0.06
	Fall	0.87	0.09
	Winter	1.00	0.00
	Annual	0.78	0.10

Table 4.4. Monthly survival estimates of adult greater sage-grouse females, 2001 and 2002, in northwest Colorado.

Month	2001 (<i>n</i> = 35)				2002 (<i>n</i> = 59)			
	Survival Estimate	Standard Error	95 % Confidence Interval		Survival Estimate	Standard Error	95 % Confidence Interval	
			Lower	Upper			Lower	Upper
April	0.97	0.03	0.82	1.00	0.92	0.04	0.81	0.96
May	0.94	0.04	0.79	0.99	0.85	0.05	0.73	0.92
June	1.00	0.00	1.00	1.00	0.93	0.04	0.81	0.98
July	0.88	0.06	0.71	0.95	0.95	0.03	0.83	0.99
August	0.96	0.04	0.79	1.00	1.00	0.00	1.00	1.00
September	1.00	0.00	1.00	1.00	0.95	0.04	0.82	0.99
October	0.89	0.06	0.71	0.96	0.85	0.04	0.81	0.99
November	1.00	0.00	1.00	1.00	0.97	0.03	0.81	1.00
December	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00
January	1.00	0.00	1.00	1.00	0.88	0.06	0.71	0.95
February	0.96	0.04	0.75	0.99	0.91	0.06	0.70	0.98
March	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00

Table 4.5. Monthly survival estimates of yearling greater sage-grouse females, 2001 and 2002, in northwest Colorado.

Month	2001 (<i>n</i> = 27)				2002 (<i>n</i> = 18)			
	Survival Estimate	Standard Error	95% Confidence Interval		Survival Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper			Lower	Upper
April	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00
May	1.00	0.00	1.00	1.00	0.94	0.05	0.69	0.99
June	0.92	0.05	0.74	0.98	0.94	0.06	0.68	0.99
July	0.88	0.07	0.68	0.96	1.00	0.00	1.00	1.00
August	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00
September	1.00	0.00	1.00	1.00	0.94	0.06	0.66	0.99
October	0.95	0.04	0.74	0.99	0.93	0.06	0.65	0.99
November	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00
December	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00
January	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00
February	0.90	0.06	0.69	0.98	1.00	0.00	1.00	1.00
March	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00

Table 4.6. Breeding, brood-rearing, fall and winter survival models varying by year, age and year + age for greater sage-grouse females in Moffat County, Colorado, 2001/2002. Models with $\Delta AIC_c \leq 2$ are considered competing models.

Season	Model	AIC _c	ΔAIC_c	# Parameters	Deviance
Breeding	{S (a + t)} ^c	110.5	0.0	3	104.4
	{S (t)} ^a	112.4	1.9	2	108.4
	{S (a)} ^b	112.6	2.1	2	108.5
	{S (.)} ^d	116.5	6.0	1	114.5
Brood-rearing	{S (t)} ^a	83.6	0.0	2	79.5
	{S (.)} ^d	83.9	0.3	1	81.9
	{S (a + t)} ^c	85.6	2.1	3	79.5
	{S (a)} ^b	85.9	2.4	2	81.8
Fall	{S (.)} ^d	68.1	0.0	1	66.0
	{S (t)} ^a	69.9	1.8	2	65.8
	{S (a)} ^b	70.0	1.9	2	65.9
	{S (a + t)} ^c	71.9	3.8	3	65.7
Winter	{S (.)} ^d	65.5	0.0	1	63.5
	{S (a)} ^b	66.0	0.5	2	61.9
	{S (t)} ^a	67.2	1.7	2	63.1
	{S (a + t)} ^c	70.0	2.5	3	61.7

^a Variation due to year

^b Variation due to age

^c Variation due to year and age

^d No variation due to year or age

Table 4.7. Annual survival models varying by year, age, season and time trend for greater sage-grouse females in Moffat County, Colorado, 2001/2002. Models with $\Delta \text{QAIC}_c \leq 2$ are considered competing models.

Model	QAIC _c	ΔQAIC_c	# Parameters	Deviance
{S (.)} ^c	138.3	0.0	1	136.3
{S (a)} ^b	138.4	0.1	2	134.4
{S (t)}	139.6	1.2	2	135.6
{S (T)} ^d	140.0	1.7	2	136.0
^a {S (a + t)}	140.1	1.7	3	134.0
{S (a + T)}	140.2	1.8	3	134.1
{S (a * T)}	142.1	3.7	4	134.0
{S (s)} ^e	144.0	5.6	4	136.0
{S (a + s)}	144.1	5.8	5	321.2
{S (a * s)}	144.1	5.8	5	134.0

^a Variation due to year

^b Variation due to age

^c No variation due to year or age

^d Variation due to seasonal time trend

^e Variation due to season

CHAPTER 5. FITNESS OF GREATER SAGE-GROUSE FEMALES ASSOCIATED WITH DISEASE AND PRE-NESTING BODY CONDITION IN NORTHWEST COLORADO

INTRODUCTION

Body Condition

Condition is a term that describes the fitness of an individual to cope with its present and future needs (Owen and Cook 1977). Condition indices are used to adjust body weights of birds with structural size differences and should reflect the relative fitness of the individual (Bailey 1979). Individuals in good condition (those with high energy reserves) should exhibit greater probabilities of survival and reproduction than individuals in poor condition (Hepp et al. 1986, Reynolds et al. 1988). The proximate controls of reproduction operate through the energy available to reproducing birds thus the role of female condition is critical in determining reproductive effort (Krebs 2001).

Remington and Braun (1988) investigated carcass composition of greater sage-grouse during the winter in North Park, Colorado. Greater sage-grouse gained weight over the winter, presumably for breeding and nesting activities in spring. Barnett and Crawford (1994) linked maternal nutrition to productivity in greater sage-grouse, however they provided no specifics on blood parameters or body condition indices of females in good condition. Beck and Braun (1978) conjectured that differential survival in greater sage-grouse might be weight-related. I assessed body condition of greater sage-grouse in northwestern Colorado by using a body condition index that adjusted for body size and a

biochemistry panel. These parameters were assessed for their influence on reproduction and survival.

Biochemistry

Few studies dealing with plasma biochemistry and physiology in wild birds can be found in the scientific literature. Most research papers have dealt with domestic or captive birds kept in zoos, rehabilitation facilities, or research centers (Sturkie 1976, Gee et al. 1981, Redig 1993). Normal reference values of blood chemical constituents are known only for 5% of bird species and have been studied mostly in captive situations (Ferrer 1993). Currently there are no published data indicating reference values for greater sage-grouse, thus this study and research being conducted in Oregon and Nevada (M. Dunbar, personal communications) will be important in defining these reference ranges for pre-laying females. The knowledge of normal reference values in plasma for wild species is important as it may provide insights into the health of individuals, quality of diet and suitability of habitat (Gavett and Wakeley 1986). Normal blood parameter reference values for endangered species involved in reintroduction or restoration programs are important in order to better understand the physiological status of the released birds. Additionally, serum chemistry is routinely used for the detection of organ disease in domestic mammals and is becoming more common for avian patients (Campbell and Coles 1986). A biochemistry panel can help identify the occurrence and severity of diseases, or to confirm disease diagnosis (Ritchie et al. 1994).

Factors such as age (Sturkie 1976), sex (Perry et al. 1986), captivity (Dobado-Berrios et al. 1998), diet (Gavett and Wakeley 1986, Ferrer 1993) and reproductive status (Beckerton and Middleton 1982, Cain et al. 1982, White et al. 1987) can influence the total variation

found in metabolites, electrolytes and other organic molecules. However, presently these factors are poorly understood due to difficulty of gathering information on different age-classes in wild species. Research has also indicated that the physiological condition of birds can influence serum chemical constituents (Dolnik 1973, Driver 1981). Therefore, the biochemistry panel of female greater sage-grouse entering the reproductive period may be an indicator of physiological condition and thus may influence productivity or survival rates.

Diseases

Serology tests examine contagious diseases transmissible to and from domestic fowl. Little is known how or if these domestic diseases affect wild avian populations. Avian influenza can cause anorexia, labored breathing, diarrhea, swelling and death in game birds (Wobeser 1997, Keramas 2002). *Salmonella* spp. can cause emaciation, respiratory problems, loss of coordination and death in birds (Steele and Galton 1971). Three important *Mycoplasma* species known to poultry are *M. gallesepticum*, *M. synoviae*, and *M. meleagridis*. Transmission of *Mycoplasma* spp. occurs through direct contact or airborne droplets and can be transferred through the eggs from female to progeny (Wobeser 1997). *M. gallesepticum* is a known pathogen of upland game birds raised in captivity and causes airsacculitis in chickens (*Gallus domesticus*) and sinusitis in turkeys (Yoder 1991). *M. synoviae* causes respiratory disease and synovitis in domestic poultry (Kleven et al. 1991). *M. meleagridis* has been known to affect the respiration and growth in juvenile turkeys (Yamamoto 1991). *M. meleagridis* occurs in wild turkeys, however, reports of occurrence in other upland game birds have not been confirmed. It has been speculated that *Mycoplasma* spp. could cause major die-offs and impaired reproduction and survival in sage-grouse (Braun et al. 1994).

As available habitat decreases in size and animals are forced into areas of high densities, disease outbreak may become more prevalent (Braun et al. 1994). Additionally, the gregarious nature of greater sage-grouse could facilitate disease transmission. A reduced body condition may make a host slower, weaker and thus more vulnerable to other mortality factors (Atkinson and Van Riper III 1991, Hudson and Dobson 1991). Diseases, body condition and serum chemistry of greater sage-grouse in northwest Colorado are unknown. My objectives were to (1) investigate pre-breeding season body condition through assessment of a condition index and a biochemistry panel, (2) estimate disease prevalence, and (3) relate body condition and disease prevalence to reproductive parameters and survival rates during breeding and brood-rearing.

METHODS

Females were captured from 27 March to 26 April in 2001 and from 25 March to 12 April 2002 using spot-light techniques and a CODA net-launcher. At the time of capture, 2 ml of blood were taken from 81 females (43 adults and 38 yearlings) and 34 males. Bleeding was done from the cutaneous ulnar vein using 22 and 26-gauge needles attached to a 3 cc syringe (Campbell and Coles 1986). Prior to puncture, alcohol was used to clean the skin. Blood samples were placed into sterile tubes; red-topped tubes without anticoagulant and lithium-heparin tubes. Serum for the biochemical analysis was centrifuged at 3000 rpm for 10 minutes and frozen until analysis at Washington State Clinical Pathology Laboratory. The blood chemistry profile indicated aspartate amino transferase (AST), alkaline phosphatase (AP), creatinine phosphokinase (CK), cholesterol, glucose, total protein, creatinine, phosphorous, sodium, potassium, chloride, and uric acid. Calcium was measured only in

2002. The serum for disease analysis was sent both as fresh and frozen samples to the Colorado Veterinary Diagnostic Laboratory at Colorado State University to determine whether storage methods would alter disease results. Diseases were screened using a plate agglutination test. Additionally, 15 samples were sent to the Animal Health Laboratory of the Idaho Department of Agriculture, Boise. Both male and female grouse were tested for avian influenza, *S. pullorum*/ *S. typhoid*, *M. gallisepticum*, *M. synoviae*, and *M. meleagridis* using the plate agglutination tests. Morphological characteristics of females were measured at time of capture and included mass and keel length. Mass was measured using 5000g electronic scales. Keel bone length was measured using calipers.

I monitored females until nesting was evident (Chapter I). When a nest was found mid-laying, I determined the date of clutch initiation by backdating from the hatch date and using a laying rate of 2 eggs per 3 days (Schroeder et al. 1999). A hand-held Yagi antenna, attached to a receiver/scanner, was used to monitor the radio-tagged grouse. Each female was monitored 1-2 times a week throughout the spring and summer to 31 August to estimate breeding and brood-rearing survival.

Reproductive Parameters

Body Condition Index.

No linear relationship existed between body mass and days to initiate egg-laying ($F = 0.40$, $P = 0.529$, $r^2 = 0.01$) therefore, to estimate pre-laying body condition, I used the equation $\text{body mass} \times \text{keel}^{-3}$, defined by Johnson and Boyce (1990). The influence of body condition on nest initiation and nest success was estimated using ANOVA. Analysis of the relationship between body condition indices and initiation date, clutch size, and hatch size

(number eggs which hatched) was estimated by linear regression (McClave and Dietrich 1994).

Biochemistry.

Simple linear regression was used to estimate whether there was a trend in biochemical values as hens approached nest initiation (range: 3-43 days). Serum chemical constituents were compared between ages (yearling or adult), years, capture technique and the interactions among variables using a 3-way factorial multivariate analysis of variance (MANOVA). Missing values were replaced by the mean value for that variable (Ott and Longnecker 2001). Calcium was not included in this analysis, as values had only been collected in 2002. Evaluation of univariate ANOVA and canonical analysis was used to determine which variables contributed to overall differences.

Protein, phosphorous, AP, creatinine, calcium and cholesterol have been associated with egg-laying in birds (Ritchie et al. 1994). Forward step-wise logistic regression was used to model the importance of these serum chemical constituents in predicting each of 2 binary variables; nest initiation and nest success (Beier 1989). Multiple regression models were used to predict the importance of the biochemistry panel in predicting clutch initiation date, clutch size and hatch size. A significance level of $P \leq 0.10$ was used to determine which variables entered and remained in the model. Calcium was analyzed separately as only 1 year of data was available. Nest initiation and success were analyzed using ANOVA and simple linear regression was used to analyze clutch initiation and clutch size. All analyses were performed in SAS 8.2 (SAS Institute 1999).

Diseases.

Relationship of prevalence of disease and nest initiation and nest success was determined through a chi-squared goodness of fit test (McClave and Dietrich 1994). Associations between nest initiation date and clutch size were determined through t-tests (Snedecor and Cochran 1980). Forward step-wise logistic regression was used to model the importance of the body condition index or serum chemical constituents in predicting disease presence or absence. Age and year were included as class variables.

Survival

Body Condition.

Female survival was analyzed for breeding and nesting (1 April to 15 June) and brood-rearing (16 June to 31 August). To assess whether variation in survival coincided with biochemical values, body condition indices, or disease prevalence, I used individual encounter histories with covariates and incorporated them into the design matrices in program MARK (White and Burnham 1999). Missing individual covariate values were assigned the mean of the variable (Ott and Longnecker 2001). The QAICc statistic for small populations was used to select the best model among alternative parametric models (Burnham and Anderson 1998). Assessment of the data showed evidence of overdispersion ($\hat{c} = 1.38$) (Anderson et al. 1994). A model was first selected to determine whether survival ratios differed among ages, seasons, years, or none of these parameters. Next, a set of *a priori* models were developed under the guidance of current avian nutrition literature models. They were constructed upon the best of the aforementioned models and incorporated the body condition index and blood parameters as covariates in design matrices.

The variables that were included in the models included the body condition index, total protein, uric acid, cholesterol, glucose, potassium, sodium and phosphorous. Serum protein levels for bird species range between 2-6 grams/ 100ml (Campbell and Coles 1986, Redig 1993, Lumeij 1997). Low protein levels can indicate chronic disease, malnutrition, malabsorption, chronic blood loss and starvation. Elevated protein levels indicate dehydration, shock, chronic disease, trauma or infection (Pesek 1996). Mean protein value for greater sage-grouse hens in Oregon and Nevada was 5.3 g/dl (M. Dunbar, personal communications). Age and diet may influence uric acid concentration in the blood, a product of nitrogen and protein catabolism (Ritchie et al. 1994). Cholesterol concentrations vary with diet, particularly protein uptake (Ritchie et al. 1994). Potassium is necessary for muscle activity, and protein synthesis (Redig 1993). Elevated glucose levels can indicate malnutrition, bacterial infections, hormonal problems, stress, and diabetes (Pesek 1996). Both sodium and potassium help maintain the body's fluid balance (Ritchie et al. 1994). Mean phosphorous level for pre-laying hens in Oregon was 7.3 mg/dl ($n = 144$) (M. Dunbar, personal communication). Elevated levels can indicate renal disease, and starvation (Campbell and Coles 1986).

Survival rates were estimated using program MARK (Chapter 4) for the first month after capture for individuals captured by the CODA net-launcher and night spotlighting. Models were analyzed to determine whether capture technique influenced survival. AICc was used to select the best model as no overdispersion was detected in this data set ($\hat{c} < 1.00$).

Diseases

Survival models were also estimated using program MARK for those individual greater sage-grouse tested for *M. synoviae*. The association of disease prevalence with survival was tested against the model in which survival did not vary with disease prevalence. QAICc was used to select the best model as the data were adjusted for overdispersion ($\hat{c} = 1.33$). The model with the lowest QAICc value was chosen as the model which best fit the data.

RESULTS

Reproductive Parameters

Body Condition Index.

The mean body condition index in 2001 was 0.0015, $SD = 0.003$ ($n = 43$), which did not differ ($F = 0.76$, $P = 0.388$) from 2002 (0.0015, $SD = 0.002$, $n = 38$). The mean body condition index for adults was 0.0015, $SD = 0.0003$ ($n = 47$), and did not differ ($F = 2.16$, $P = 0.147$) from that for yearling females (0.0014, $SD = 0.0002$, $n = 34$). Body condition did not influence nest initiation rates ($F = 0.51$, $P = 0.477$, $n = 73$) or nest success ($F = 0.42$, $P = 0.520$, $n = 60$). Additionally, clutch size, hatch size and nest initiation dates were not related to the body condition index (Table 5.1).

Biochemistry.

Simple linear regression indicated no trend in serum biochemistry as females neared nest initiation ($r^2 < 0.40$). Therefore, females were pooled, regardless of breeding stage. No differences in the biochemistry panel were detected for year*age* capture (Wilk's $\lambda = 0.89$; $F = 0.73$; 12,68 df; $P = 0.717$), year*age (Wilk's $\lambda = 0.79$; $F = 1.48$; 12,68 df; $P = 0.153$), year*capture (Wilk's $\lambda = 0.58$; $F = 0.87$; 12,68 df; $P = 0.577$), age*capture (Wilk's $\lambda = 0.91$;

$F = 0.57$; 12,68 df; $P = 0.856$) or age (Wilk's $\lambda = 0.87$; $F = 0.84$; 12,68 df; $P = 0.605$). There was, however, a difference detected between years (Wilk's $\lambda = 0.43$; $F = 7.25$; 12,68 df; $P < 0.001$). Creatinine ($F = 49.49$, $P < 0.001$), total protein ($F = 24.88$, $P < 0.001$), cholesterol ($F = 16.63$, $P < 0.001$), and AP ($F = 5.70$, $P = 0.019$) were the factors driving the difference between years (Table 5.2). All values were greater in 2002 than in 2001. Additionally, analysis revealed differences due to capture techniques (Wilk's $\lambda = 0.65$; $F = 3.08$; 12,68 df; $P = 0.002$). Trapping with the CODA net-launcher resulted in elevated levels of CK ($F = 7.01$, $P = 0.010$) and chloride ($F = 12.05$, $P = 0.001$) (Table 5.3).

None of the biochemical constituents entered the logistic regression equations as significant predictors of nest initiation or success. Similarly, none of the variables entered the multiple regression equations as significant predictors of initiation date, clutch size or hatch size. Calcium was not associated with nest initiation ($F = 1.07$, $P = 0.311$, $n = 26$), clutch initiation date ($F = 0.03$, $P = 0.85$, $r^2 = 0.002$, $n = 19$), nest success ($F = 0.46$, $P = 0.803$, $n = 22$), or clutch size ($F = 1.14$, $P = 0.30$, $r^2 = 0.081$, $n = 15$).

Diseases.

There was no difference ($P = 1.000$) in fresh and frozen sample results for *M. gallesepticum* ($n = 22$), *M. meleagridis* ($n = 22$), *S. pullorum*/*S. typhoid* ($n = 20$), or avian influenza ($n = 25$). There was 89% consistency for results of fresh and frozen samples tested for *M. synoviae* ($n = 18$). Serum samples were divided and sent to 2 separate labs to determine the consistency in results. There was 100% consistency for *M. gallesepticum* ($n = 15$), *M. meleagridis* ($n = 15$), *S. pullorum*/*S. typhoid* ($n = 15$) and avian influenza ($n = 15$) and a 93% consistency for *M. synoviae* ($n = 15$).

The serology analysis in 2001 indicated a 55% occurrence of *M. synoviae* for females ($n = 31$) and 92% presence for males ($n = 12$). In 2002, the occurrence of *M. synoviae* was only 12% ($n = 33$) and 6% ($n = 18$) for females and males, respectively. There was no difference between prevalence in adult females (45%, $n = 38$) and yearling females (67%, $n = 21$) ($t = -0.73$, $P = 0.392$) over the 2 years. The tests were negative for *M. gallesepticum* ($n = 54$), *M. meleagridis* ($n = 56$), *S. pullorum*/*S. typhoid* ($n = 47$), and avian influenza ($n = 52$) in females over 2 years. Similarly, males tested negative for *M. gallesepticum* ($n = 24$), *M. meleagridis* ($n = 24$), *S. pullorum*/*S. typhoid* ($n = 26$), and avian influenza ($n = 29$). Nest initiation, nest success, clutch initiation date and clutch size were not influenced by the presence of *M. synoviae* (Table 5.4).

Forward stepwise logistic regression found cholesterol, sodium and year as significant predictors of positive disease results. The logistic regression equation that resulted was $\text{Logit}(Y) = 33.36 - 0.02(\text{cholesterol}) - 0.20(\text{sodium}) + 0.91(\text{year}) + e$ (Table 5.5). Cholesterol and sodium was greater in grouse negative for *M. synoviae* (163.06 mg/dl, $SE = 5.98$; 155.37 mEq/l, $SE = 0.71$, $n = 30$) than those that tested positive for the disease (143.88 mg/dl, $SE = 10.36$; 154.14 mEq/l, $SE = 0.82$, $n = 14$).

Survival

Body Condition.

The model which best fit the data from the simple models of survival varying with age, season, year or none of these, was the model varying with age (Table 5.6). Therefore, subsequent complex models were built upon the age parameter. There were several competing models which best fit the data ($\Delta \text{QAICc} \leq 2$). These included survival varying with age + uric acid, survival varying with age + body condition index, and survival varying

with age + protein (Table 5.6). Survival rates in the first month post-capture were 0.90, $SE = 0.03$, $n = 116$ for grouse captured at night and 0.96, $SE = 0.04$, $n = 26$ for grouse captured by the CODA net-launcher. Capture effects did not explain the data ($\Delta AICc \geq 2$) better than the null model.

Diseases.

The model which best fit the data for females tested for *M. synoviae* was the null model, survival that did not vary with disease prevalence. The difference in QAICc was just slightly > 2 , indicating there is weak evidence that the 2 models are not competing (Burnham and Anderson 1998) (Table 5.7).

DISCUSSION

Body Condition Index

My results detected no relationships between body condition indices, nest initiation rate, nest success, initiation date, clutch size or hatch size. These may not have been detectable as the range for body condition indices for yearling (0.0011 - 0.0018) and adult females (0.0010 - 0.0020) was narrow. Similarly, no correlation was evident between body condition (adjusted for reproductive status and body size) and clutch initiation dates and clutch size for willow ptarmigan (*Lagopus lagopus*) populations in British Columbia and Manitoba (Robb et al. 1992). Additionally, no associations were made between clutch size and hen weights for ruffed grouse or prairie chickens (*Tymphanuchus cupido*) in Minnesota (Maxson 1974, Bergerud 1988).

Alternatively, Breitenbach et al. (1963) showed concomitance between female weight and clutch initiation date and clutch size for ring-necked pheasants. Winter weight of

pheasants in Ohio was also associated with productivity (Edwards et al. 1964). Likewise, research by Porter et al. (1983) on turkeys in Minnesota indicated the weight of females to be highly related to productivity. A study on white-tailed ptarmigan (*Lagopus leucurus*) indicated female body condition was associated with the length and frequency of incubation breaks, presumably associated with nest success (Weibe and Martin 1997). Studies have indicated, and my research supports the notion (Chapter 4), that greater sage-grouse suffer the highest natural mortality in the spring and summer (Wallestad 1975, Connelly et al. 1994, Connelly et al. 2000). Beck and Braun (1978) showed that greater sage-grouse females gained weight from September to April. My data illustrated that the spring condition of greater sage-grouse females, based on a body condition index, did not limit reproduction in 2001 or 2002.

Pre-breeding body condition index was a predictor of survival through the breeding and brood-rearing periods. Kabat et al. (1956) observed a direct correlation between fat stores and body weight and the ability of female ring-necked pheasants to resist stress. Similarly, heavier female pheasants and turkeys showed higher survival rates (Edwards et al. 1964, Porter et al. 1983). Robb et al. (1992) observed no relationship between willow ptarmigan female body condition and reproductive parameters but noted females in poor condition exhibited lowered survival probabilities. Similarly, greater sage-grouse in poor condition pre-breeding appear to invest fully in reproduction, at the expense of reduced survival during breeding and brood-rearing.

Biochemistry

The biochemistry panel for females in northwest Colorado was comparable to values collected in Oregon and Nevada except for AST and uric acid levels (M. Dunbar, personal

communication) (Table 5.2). Uric acid levels for my population of greater sage-grouse fell within the range of mean uric acid levels for 12 species of captive birds at the Patuxent Wildlife Research Center (6.9 - 12.4 mg/dl) (Gee et al. 1981). AP, cholesterol, creatinine, sodium, potassium and chloride are elements with which no reference values exist for greater sage-grouse. I compared these values to the range of mean values acquired for the 12 captive species (Gee et al. 1981). All my results fell within the range of means reported except chloride. The levels of chloride for the 12 captive species ranged from 99 - 112 mEq/l, while the mean value for greater sage-grouse females was 119 mEq/l. Chloride levels fall within a narrow range in avian species (Ritchie et al. 1994) and reasons for the elevated levels are unknown. My results indicated that biochemistry constituents did not vary between ages, but showed disparity due to year and capture technique.

Creatinine, cholesterol, protein and AP exhibited higher levels in 2002 than in 2001. Creatinine is minimally affected by dietary or tissue proteins and is insensitive as a diagnostic test (Ritchie et al. 1994). Elevated creatinine levels have been described in connection with egg-laying (Ritchie et al. 1994). Age, heredity, nutrition and diseases affect cholesterol levels in avian blood, which range from 100 to 200 mg/dl in healthy birds (Campbell and Coles 1986, Redig 1993). Cholesterol concentrations vary with a bird's diet and are linked to diets higher in protein sources (Ritchie et al. 1994). Low protein levels can indicate chronic disease, malnutrition, malabsorption, chronic blood loss and starvation. Total protein concentrations in female birds increase just prior to egg-laying (Lumeij 1997). In mourning doves (*Zenaida macroura*) cholesterol and protein concentrations were associated with attainment of puberty and reproductive potential (White et al. 1987). In birds, increased AP activity is associated with increased osteoblastic activity such as skeletal

growth and impending ovulation (Campbell and Coles 1986, Lumeij 1997). AP levels may be elevated due to irritation of cells in different tissues yet have no specific importance (Ritchie et al. 1994).

The elevated biochemical levels in 2002 may be associated with egg-laying or diet. January - March of 2002 experienced 1/3 less precipitation in the form of snow than 2001 (Appendix 1-B). Thus vegetation and invertebrates were earlier to emerge in 2002. For this reason, although sampling dates were relatively consistent among years, biochemistry values may have increased in association with forbs and invertebrates in the diet. Additionally, clutch initiation was earlier in 2002 (Chapter I) and thus females may have been at a later reproductive stage although they were sampled at equivalent dates.

Differences related to capture technique may be due to variation associated with diurnal changes in blood (Dolnik 1973) or differential stress. Creatinine kinase (CK) and chloride levels were greater for females captured by the CODA net-launcher than those captured by spot-light trapping. The physiological influence of serum chloride is poorly understood in birds, however ranges are typically narrow (Ritchie et al. 1994). Chloride levels may not have any biological relevance to capture for greater sage-grouse, however, elevated chloride levels due to the stress of capture have been reported in grizzly bears (*Ursos arctos*) (Brannon 1985). Elevated levels of creatinine kinase may be as a result of the excitement of handling (Lumeij 1997) or due to elevated exercise prior to handling. Plasma CK levels in turkeys were sensitive to handling and stress (Lumeij 1997). It is doubtful that CK levels are associated with the time of capture as elevations are typically seen due to muscle cell damage (Ritchie et al. 1994). The CODA net-launcher was deployed on leks within the first hours of daylight and was set to capture females surrounding the dominant

male. Mean number of individuals captured was 3.1 (range: 1-10, $n = 8$), thus individual processing time was lengthened and may have produced increased stress in grouse. Despite, the apparent increase in stress due to use of the CODA net-launcher, the use of this technique did not influence survival rates within 1 month post-capture.

None of the biochemistry elements measured were significant predictors of any of the reproductive parameters measured. For black grouse (*Tetrao tetrix*) losses during incubation are most likely attributed to predation, while factors such as climate, maternal condition, or nest site availability are of minor importance (Angelstam 1984). Contrastingly, Wittenberger (1978) argued that viability of grouse eggs and chicks are correlated with condition of incubating hens, presumably associated with spring forage conditions. Greater sage-grouse in the Axial Basin and Danforth Hills exhibited above average nest success and comparable clutch sizes to other populations of greater sage-grouse across the range of the species (Chapter 1). Given these results, it does not appear that pre-breeding body condition is limiting reproduction.

Survival models with the biochemistry panel as a gauge of pre-breeding condition may give an indication of the diet and habitat available to females. The models indicated that protein and uric acid were important parameters in greater sage-grouse survival. Protein levels are greatest in forbs (Peterson 1970) and invertebrates and have been used to diagnose malnutrition (Perry et al. 1986). Protein deficiencies resulted in decreases in body mass of northern bobwhite and scaled quail (Giuliano et al. 1996). Plasma uric acid is the major nitrogen excretory product in birds and is an index of protein catabolism. Serum concentrations are coupled with protein utilization and long-term fasting in avian species (Cherel et al. 1987, Boismenu et al. 1992). Although I did not directly study the diet of the

greater sage-grouse population in the Axial Basin and the Danforth Hills, it was observed that total serum protein and uric acid were important in modeling survival. Uric acid and protein levels may be associated with forbs and invertebrates in the diet and could potentially be influencing survival of greater sage-grouse females during breeding and brood-rearing.

Diseases

There was an 89% consistency for results of fresh and frozen samples tested for *M. synoviae* and a 100% consistency for results of the other diseases tested. To validate laboratory results, serum samples were divided and sent to 2 separate laboratories. There was a 93% consistency for *M. synoviae* and a 100% consistency for results of the other diseases tested. The serology analysis in 2001 indicated a 55% occurrence of *M. synoviae* for females and 92% presence for males. In 2002, the laboratories were asked to test initially for *M. synoviae* and then test for the remaining pathogens. The occurrence of *M. synoviae* was only 12% and 6% for females and males, respectively. Three females were re-captured in 2002, and all were consistently negative for *M. synoviae* between years. No other pathogens tested for were positive over the duration of the study. Both laboratories used a plate agglutination screening test provided by the same company. This test is not as accurate as a hemoagglutination inhibition test (K. Eyre, personal communication). The assessment works on the premise of antigen complement binding with the disease and has 85% specificity and 91% sensitivity. *M. synoviae* is smaller than the other *Mycoplasma* spp., thus making it more susceptible to false positives when the antigen creates a clumped lattice with red-blood cells, rather than the pathogen. Additional testing (hemoagglutination inhibition test) and culturing samples from individuals testing positive for the disease would be required in order to accurately determine disease prevalence.

Braun et al. (1994) speculated that *Mycoplasma* could potentially cause impaired reproduction and survival in sage-grouse. My results failed to confirm this, although the statistics were based on questionable disease incidence. I found no relationship between *M. synoviae* and nest initiation, clutch initiation date, clutch size or nest success. Ritchie et al. (1994) found that the majority of the reproductive system in chickens function similarly in *Mycoplasma* infected birds as those without *Mycoplasma*. Survival of greater sage-grouse during the breeding and brood-rearing period also did not vary with occurrence of *M. synoviae*.

Blood biochemistry values were used to understand the physiological status of the grouse infected with *M. synoviae*. Sodium and cholesterol levels were the only predictors of positive disease results and the levels were less in grouse testing positive for *M. synoviae*. Sodium values are maintained within narrow limits in birds and thus differences may indicate a pathological condition, however this is rarely seen in avian patients (Ritchie et al. 1994). Cholesterol concentrations are usually lower in stressed mammals but have been reported as elevated in stressed canvasbacks (*Aythya valisineria*) (Perry et al. 1986). Assuming that individuals positive for *M. synoviae* had greater physiological stress, they exhibited the same trends in cholesterol as mammals. However, the diagnostic value of sodium and cholesterol in birds is poor (Ritchie et al. 1994), and these statistics are based on inconclusive evidence of disease, thus these results should be viewed cautiously.

No clinical symptoms of *M. synoviae* were detected during handling. Hoffman et al. (1997) were also not able to confirm the presence of *M. gallesepticum* or *M. synoviae* through culturing for wild turkeys in west-central Colorado and concluded that false positives had been reported. Forty-three percent of their birds tested positive for either of these

pathogens ($n = 51$). Given there was 0 occurrence for avian influenza, *S. pullorum*/ *S. typhoid*, *M. gallisepticum*, and *M. meleagridis*, these diseases appear not to be a major threat to the greater sage-grouse populations in the area. Possible explanation for the inconsistency in *M. synoviae* from 2001 to 2002 could be an indication that the tests were giving a higher percentage of false positives in 2001 due to different sampling protocol, or the disease was present at a higher level in 2001. The absence of clinical signs, large variation in disease prevalence between years, inconsistency in results due to freezing and between labs, the variable nature of the plate agglutination test, and no influence on reproductive and survival parameters suggests incidence of *M. synoviae* in greater sage-grouse females is inconclusive. Analysis of biochemical values indicated that birds positive for *M. synoviae* might have experienced physiological affects, although sodium and cholesterol have poor diagnostic value and these statistics are based on uncertain results. Due to these confounding results, I recommend that future research examine the physiological response of greater sage-grouse females experimentally infected with *M. synoviae*.

MANAGEMENT IMPLICATIONS

Reference serum chemical ranges of greater sage-grouse are important for predicting physiological and pathological condition of birds. Future research needs to estimate serum chemical ranges for chicks, males and females year-round. Measures of body condition did not appear related to reproductive parameters but were associated with survival. Particularly important predictors of survival were the body condition index, uric acid and protein levels, factors that may fluctuate with diet. Invertebrate abundance varies with herbaceous cover (Jamison et al. 2002) and precipitation (Crawford 1981), thus limitations of invertebrate

biomass due to drought or habitat quality may lead to reduced survival of greater-sage grouse during the reproductive period. This re-emphasizes the importance of maintaining native forb species in pre-breeding and breeding habitats (Chapter 1, Chapter 3).

With increasing attention on handling potentially threatened or endangered sage-grouse species, biologists need to be aware of acute stress on trapped birds, particularly those considered for translocation or detained for study. Use of the CODA net-launcher as a capture method appears to be more stressful than night spotlighting on individuals although effects may be short-term as there did not appear to be an association with capture technique and survival of individuals 1 month post-capture. However, influences of such stress on the survival and success of translocated grouse is unknown.

The population of greater sage-grouse in the Axial Basin and Danforth Hills does not appear to be infected with avian influenza, *Salmonella pullorum*/ *S. typhoid*, *Mycoplasma gallisepticum*, or *M. melagridis*. Although individuals tested positive for *M. synoviae*, I am unable to say that they were infected with the disease. To determine any impacts of the disease, individuals need to be experimentally injected with the pathogen and then associated with body condition, serum chemical constituents and fitness measures.

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Table 5.1. Coefficient of determination (r^2) for impact of spring body condition on reproductive parameters of greater sage-grouse females in Axial Basin and Danforth Hills, Colorado, 2001/2002.

Parameter	n	F	P	r^2
Clutch initiation date	43	0.68	0.415	0.016
Clutch size	52	0.01	0.938	0.001
Hatch size	32	0.02	0.883	0.001

Table 5.2. Blood biochemistry values for adult and yearling greater sage-grouse females captured in March and April, Axial Basin and Danforth Hills, Colorado, 2001/2002 and for Oregon and Nevada captured 1999-2001.

Blood Parameter (units)	Axial Basin and Danforth Hills				Oregon and Nevada (Dunbar 2002, personal communication)	
	2001		2002		Combined years and ages	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
AST (U/L) ^a	353.8 (n=50)	39.7	334.2 (n=38)	49.9	430 (n=144)	77
CK ^b (U/L)	2563.4 (n=50)	2440.9	1992.0 (n=38)	1533.4	2396 (n=143)	1017
Glucose (mg/dl)	352.1 (n=50)	49.3	339.7 (n=37)	48.9	320 (n=144)	35
Total protein (mg/dl)	4.2 (n=47)	0.6	4.9 (n=38)	0.5	5.3 (n=139)	1.2
Phosphorous (mg/dl)	6.4 (n=46)	1.8	7.2 (n=38)	2.5	7.3 (n=144)	2.4
Uric acid (mg/dl)	10.9 (n=49)	3.5	10.9 (n=38)	6.0	5.4 (n=143)	2.2
Calcium (mg/dl)	Not tested		25.6 (n=38)	6.9	21.4 (n=141)	7.4
AP ^c (U/L)	483.9 (n=52)	224.7	609.3 (n=38)	245.6	Not tested	
Cholesterol (mg/dl)	135.3 (n=49)	34.3	174.5 (n=38)	40.8	Not tested	
Creatinine (mg/dl)	0.4 (n=44)	0.1	0.8 (n=38)	0.2	Not tested	
Sodium (mEq/l)	155.0 (n=42)	2.7	154.9 (n=31)	3.9	Not tested	
Potassium (mEq/l)	4.6 (n=44)	1.6	4.6 (n=35)	1.2	Not tested	
Chloride (mEq/l)	119.0 (n=42)	6.5	119.1 (n=31)	6.5	Not tested	

^a AST = aspartate amino transferase

^b CK = creatinine phosphokinase

^c AP = alkaline phosphatase

Table 5.3. Biochemistry values for 2 capture methods (mean and standard error) in pre-laying greater sage-grouse females in northwest Colorado, 2001/2002.

Biochemistry panel	CODA Net Launcher		Spotlight trapping		F-value	P-value
	Mean	SE	Mean	SE		
CK ^a	3642.6 (n = 22)	780.8	1874.6 (n = 66)	110.9	11.52	0.001
Chloride	124.1 (n = 19)	0.6	117.3 (n = 54)	0.9	19.18	< 0.001

^a creatinine phosphokinase

Table 5.4. The influence of *M. synoviae* on reproductive parameters (mean and standard error) of greater sage-grouse females in the Axial Basin and Danforth Hills, Colorado, 2001/2002.

	Nest initiation rate	Nest success	Mean clutch initiation date	SE	Mean clutch size	SE
Positive <i>M.</i> <i>synoviae</i>	75% (<i>n</i> = 16)	69% (<i>n</i> = 13)	24 April (<i>n</i> = 26)	1.4	6.5 (<i>n</i> = 10)	0.8
Negative <i>M.</i> <i>synoviae</i>	85% (<i>n</i> = 40)	57% (<i>n</i> = 35)	20 April (<i>n</i> = 9)	1.7	6.9 (<i>n</i> = 22)	0.3
Test statistic	$\chi^2 = 0.78$	$\chi^2 = 0.20$	$t = 1.39$		$t = 0.52$	
P-value	0.377	0.658	0.175		0.607	

Table 5.5. Logistic regression model of body condition and biochemical variables predicting the prevalence of *M. synoviae* in pre-breeding greater sage-grouse females in northwest Colorado, 2001/2002.

Dependant Variable	Parameters	Regression Coefficient (SE)	F-value	Wald's Chi-square	P-value
Presence of <i>M. synoviae</i>	Cholesterol	-0.02	0.01	3.12	0.077
	Sodium	-0.20	0.13	2.47	0.116
	Year	0.91	0.49	3.40	0.065

Table 5.6. *A priori* survival models of greater sage-grouse females during the breeding and brood-rearing period tested for association with pre-breeding body condition in northwest Colorado, 2001/2002. Models with $\Delta \text{QAIC}_c \leq 2$ are considered competing models.

Model	QAIC _c	ΔQAIC_c	Parameters	Deviance
{S (age)} ^a	82.65	0.00	2	78.57
{S (.)} ^a	82.90	0.26	1	80.88
{S (age + uric acid)}	83.90	1.25	3	77.74
{S (year)} ^a	84.11	1.46	2	80.03
{S (age + index)}	84.13	1.48	3	77.97
{S (age + protein)}	84.64	1.99	3	78.48
{S (season)} ^a	84.69	2.05	2	80.61
{S (age + sodium + potassium)}	85.68	3.04	4	77.41
{S (age + protein + phosphate)}	86.14	3.50	4	77.88
{S (age + index + sodium + potassium)}	88.29	5.64	5	77.89
{S (age + protein + cholesterol + glucose + phosphate)}	89.73	7.08	6	77.17
{S (age + index + protein + cholesterol + glucose + phosphate)}	91.70	9.06	7	76.95
S {(age + index + protein + cholesterol + glucose + uric acid + potassium + phosphate + sodium)}	96.52	13.87	10	75.00

^a models with covariates were built upon the best of these simple models

Table 5.7. Breeding and brood-rearing survival models of greater sage-grouse females tested for *M. synoviae* in northwest Colorado, 2001/2002. Models with $\Delta \text{QAIC}_c \leq 2$ are considered competing models.

Model	QAIC _c	ΔQAIC_c	Parameters	Deviance
{S (.)}	52.97	0.00	1	50.93
{S (prevalence)}	55.04	2.07	2	50.91